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Infant Social Development and Alloparenting in Free-Ranging *Lemur catta*

by

Lisa Gould (C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Infant Social Development and Alloparenting in Free-Ranging *Lemur catta* submitted by Lisa Gould in partial fulfilment of the requirements for the degree of Master of Arts.

Linda Marie Fedigan

Supervisor

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Date June 23, 1989

ABSTRACT

Social development and alloparental care of eleven free-ranging infant *Lemur catta* was examined at the Berenty Reserve, Madagascar. By 16 weeks of age, infants still occasionally suckled and were carried dorsally, but were primarily independent of their mothers. No significant differences were found with respect to infant's sex or rank in terms of frequency or type of play behaviour, maternal rejections in relation to weaning, or measures of independence; however, lower ranking infants engaged in significantly more "dependent" behaviours than did higher ranking young. It is argued that lower ranking infants may need to maintain closer proximity to the mother for a longer period of time during infancy because such individuals may not be as readily rescued in a stressful or dangerous situation as a higher-ranking infant. Sex was not found to be a factor in terms of measures of dependence. Group members of all age/sex classes were found to participate to varying degrees in alloparental care and affiliative behaviours with infants, and some types of care and interactions such as grooming of infants and social play with infants were performed significantly more frequently by animals of particular age/sex classes. Adult males, previously reported not to interact with infants, were found to occasionally groom and play with infants. Rank of the infant did not affect the amount of alloparental care it received. Suggested benefits to infants of alloparental care in this species include rescue from dangerous situations if the mother is not nearby, and opportunities to develop relationships and acquire social skills with group members other than the mother. Mothers benefit by gaining free time to forage and rest while the infant interacts with others. Through alloparenting, pre-reproductive females have the opportunity to learn

parental skills. Adult males who interact with and display caregiving behaviours towards infants may, if they are the father, be exhibiting paternal care. Furthermore, affiliation with infants may be a strategy on the part of the adult male to establish a relationship with the mother which could enhance future reproductive success.

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Introduction

The present study is an examination of infant social development and alloparental care in *Lemur catta* , a diurnal prosimian primate living in multi-male, multi-female social groups, and endemic to the island of Madagascar. The study was conducted between July and December,1987, at the Berenty Reserve, in the extreme south of Madagascar, and covered the month prior to the birth season, as well as the 16 week period immediately following the births of the infants.

The first section of chapter one examines theories which have been proposed concerning the social development of infant primates, weaning conflict, and sex differences in infant development. As well, a number of explanations which have been proposed concerning costs, benefits, and the adaptive significance of the existence of alloparental care performed by various age/sex classes of primates are outlined. In the second section, general information on the study species and research site is presented.

In chapters two and three, the results of the present study are presented, as well as discussion and implications of the findings.

Chapter 1: Theory

Section One

Social Development of Infants

Infant social development has been widely studied in many anthropoid species, and in virtually all types of primate social organization. Numerous suggestions concerning the function of socialization have been made (e.g., Poirier,1972; Fragaszy and Mitchell,1974; Poirier,1977), and analyses have been carried out on mother/infant interactions as well as the transition from the mother/infant dyad to the stage at which young primates begin to function as independent members of a social group.

The process and function of infant social development have been outlined by Poirier (1972), and Fragaszy and Mitchell (1974). Fragaszy and Mitchell suggest that the function of socialization and social development from the standpoint of the individual is to form and maintain affiliations among individual group members as well as to prepare the behavioural repertoire so that the infant is able to respond appropriately to all types of social situations. Poirier (1977) states that the process of socialization is a way of ensuring that adaptive behaviour does not have to be rediscovered in each new generation.

Although many species-specific differences exist with respect to infant social development throughout the primate order, certain general trends are evident from a survey of the social development literature. Poirier (1972) and Fragaszy and Mitchell (1974) outline the developmental stages in the non-human primate life cycle. A synthesis of their ideas is presented below.

During the first stage, or neo-natal period, the mother/infant bond is formed (Fragaszy and Mitchell,1974). The authors suggest that this attachment is critical to the infant's subsequent, broader, socialization experiences. Poirier (1972) states that during the neo-natal period, mother-infant contact is constant, continuous, and close. He argues that the importance of this particular period is directly related to the amount and kind of maternal protection and care available to the infant. Fragaszy and Mitchell (1974) note that during the first developmental stage, the infant responds in an indiscriminate way towards social objects, and that the reflexive patterns which maintain proximity and contact between the mother and infant are designed to ensure that the infant's nutritional and contact needs are fulfilled.

Fragaszy and Mitchell suggest that as the infant develops cognitive and motor skills, the emotional and biological attachment prevalent in the early part of the first stage is no longer sufficient to satisfy the infant's needs for stimulation, and thus, it begins to explore the "non-mother" environment. The authors suggest that once an infant begins independent environmental exploration, it soon becomes capable of recognizing other individuals, and develops appropriate responses to members within its social group. Although a young primate's social experiences are still influenced by maternal rank and temperament, Fragaszy and Mitchell argue that the infant can, at this stage, interact voluntarily with conspecifics other than the mother, and thus can be considered a participatory member of a social group and no longer simply a member of a closed dyad. The authors point out, however, that although the infant is able to fend for itself in a number of situations by this stage, it still seeks emotional security from the mother.

During the third period, termed the "peer socialization stage" by Poirier (1972), the young primate regularly makes contact with conspecifics other than the mother. Poirier notes that such contact at this stage primarily involves siblings, older females and age mates. He suggests that this period is characterized by the gradual waning of infantile behavioural patterns, and is marked by the weaning process. Fragaszy and Mitchell (1974) state that as infants develop peer contacts within their social groups, play groups form, and that at this stage of development, the infant tends to associate more with age mates and thus, new social responses develop including sexual patterns, appeasement gestures, and aggressive behaviours. The authors suggest that through the practice of such behaviours with peers, the development of social communications occur, which, Fragaszy and Mitchell stress, is a necessary element in the socialization process.

Parent-Offspring Conflict

The theory of parent-offspring conflict (Trivers, 1974,1985) suggests that an infant will always tend to favor a longer period of parental investment than the parent is selected to give. Trivers also postulates that the parent is selected to avoid any investment in an offspring for which the cost is greater than the benefit, as too great an investment in any particular offspring could lead to a decrease in reproductive success.

Trivers argues that initially parental investment results in a large benefit to the infant at a low cost to the parent. However, as the infant matures and becomes increasingly independent, the benefit the offspring receives from parental care tends to decrease, while the cost to the parent increases; in terms of factors

such as depletion of resources. At the point when the benefit to cost ratio is equal to one (B/C=1), Trivers suggests that the parent is selected to terminate investment in order not to incur a decrease in reproductive success. However, the offspring is still selected to continue to request parental care after the point at which the parent terminates it, and thus, conflict between parent and offspring occurs. Parent-offspring conflict has been observed to manifest itself in the form of temper tantrums and regression to infantile behaviours on the part of the infant, and rejection as well as other forms of punishment on the part of the parent, particularly during the weaning period (Trivers, 1985). Among primates, behaviour indicative of parent-offspring conflict has been observed in a number of species including baboons (Altmann,1980), langurs (Hrdy, 1977), Japanese macaques (Collinge, 1987), owl monkeys (Dixson et al. 1981), and chimpanzees (Goodall, in Trivers, 1985).

Nicholson (1982) states that nursing is one of the clearest forms of parental investment as defined by Trivers, because it enhances the infant's chances of survival and decreases the mother's immediate ability to invest in future offspring. She suggests that this is why weaning from the nipple is the most common example of parent/offspring conflict. With respect to weaning from dorsal riding, Nicholson states that the energetic cost to the mother of carrying an infant increases in direct proportion to its weight. However, she suggests that infant locomotion is also energetically expensive. Thus, Nicholson argues, it is very likely that infant carrying by the mother will be a major source of parent/offspring conflict during certain stages of infant development.

Sex Differences

Sex differences in infant behavioural development and early infant care, as well as *lack* of such differences, have been noted to occur in a number of species in which infants have been the focus of the study. (in baboons, Ransom and Rowell, 1972; Nash, 1977; Nicholson, 1982; in chimpanzees, Nicholson, 1977; in cotton top tamarins, Cleveland and Snowdon, 1984; in vervets, Lee, 1984; in rhesus macaques, Berman,1982,1984). For example, Nicholson (1982), found that free-ranging, infant male, olive baboons continued to dorsal ride for a longer period of time than did female infants. Male infants were also carried more frequently than were females. Berman (1982) suggests that in free-ranging rhesus monkey groups, sons spend less time near the mother and her companions from infancy onwards than do daughters, and that such differences in interaction increase over time. Conversely, in their study of captive cotton-top tamarins, Cleveland and Snowdon (1984) found no sex differences in behaviour of the infants studied, as well as no evidence indicating that male and female infants were treated differently by conspecifics. Lee (1984) who found sex differences in early infant care, such as female infants being rejected from the nipple earlier than males, suggests that such differences could be related to the argument that mothers should invest more in the sex with the greatest variance in reproductive success. Nicholson (1977) suggests that environmental characteristics might influence the development of independence to a different extent in male and female infants. However, Nash (1978) argues that differences in behavioural development may be due more to individual circumstances than sex of the infant.

Alloparenting

Care of infants by conspecifics other than the mother, or alloparenting, has been closely examined in many anthropoid species. Explanations concerning the costs, benefits, and adaptive significance of alloparental behaviour have been proposed by a number of primatologists including Lancaster (1972), Hinde (1974), Hrdy (1976), McKenna (1979), Zucker and Kaplan (1981), Nishida (l983), Gray (l985), and Nicholson (1987). These explanations are outlined below.

The "mother relief" explanation suggests that the mother receives the greatest benefit by having free time to forage or rest while the infant is cared for by an alloparent (Gray,1985). In species where very high energetic costs to the mother are incurred, such as in many of the New World Monkeys, it is suggested that the high degree of alloparental behaviour by multiple caregivers reduces the energetic demands on the mother (Cleveland and Snowdon, 1984). Whitten (1982, cited in Nicholson, 1987) discovered that female vervet monkeys had both longer feeding bouts and greater intake of food when infants were at a greater distance from the mother than when infants were close by or in contact. However, Hrdy (1976) argues that the mother-infant pair only benefits if such advantages offset potential disadvantages such as incompetent care, physical abuse, or kidnapping of the infant. For example, Nishida (1983) observed that among chimpanzees, mothers incur costs, rather than receive benefits, by allowing adult males access to their infants. He notes that mothers were observed to constantly attend to the male and infant during periods of male "care", thus, mothers did not receive the benefits of extra feeding or leisure time, as the "mother relief" explanation proposes.

The "learning to mother" hypothesis states that young nulliparous allomothers benefit from opportunities to care for infants before giving birth to their own (Lancaster,1972; Hinde, 1974 ; Hrdy, 1976; Nishida,1983; Gray, 1985). In fact Nicholson (1987), noting that young nulliparous females in many species perform relatively much more alloparental care than do members of other age/sex classes, suggests that allomothering appears to have a specific developmental function in young female primates. However, in this case also, allomothering may be maladaptive for the mother-infant pair, if performed by inexperienced females who care poorly for an infant (Hinde,1974).

The "adoption" explanation argues that the infant gains the primary benefit, because it has an increased chance of being adopted if the mother should die (Lancaster, 1971; Nishida,1983). Hrdy (1976) suggests that adoptions resulting from "kidnapping" of an infant by a lactating, higher ranking female who has lost her own infant may be advantageous to both the natural mother and the infant; because the natural mother is free to resume cycling, thus her reproductive success may be enhanced, and the infant benefits by an increase in its own status and better access to resources.

The "status elevation" explanation suggests that alliances between females of different ranks are created through allomothering (Nishida,1983; Gray,1985). Such alliances could prove beneficial to the lower ranking allomother in terms of better access to resources such as preferred foraging sites and sleeping areas. Cheney (1978) suggests that through frequent contact with unrelated females, via allomaternal care of infants, young females may be integrated into adult female social structure. Furthermore, an increase in rank could result in greater protection from predators, and increased mating opportunities during

the breeding season. A nulliparous female whose rank increases through alloparenting may also benefit once she herself gives birth, because if she is a member of a species in which rank correlates positively with amount of alloparental care, her infant may be more likely to receive such care than an infant of a lower ranking mother.

The "selfish allomother" hypothesis predicts that an allomother could reduce both her and her infant's competition for resources by lowering the inclusive fitness of another infant and its kin (Gray,1985). With respect to Old World Monkeys this hypothesis is stated to hold true more for cercopithecines than colobines (McKenna,1979). McKenna argues that this is because the morphology and physiology of ancestral colobines has resulted in the evolution of foraging and food-processing adaptations such that both intra-troop feeding competition and the importance of dominance among females are reduced. However, Nicholson (1987) argues that factors such as insufficient quantitative data on both female relations and allomaternal care in wild colobines, and the fact that only one species, the gray langur, has been used to represent all colobines, make McKenna's hypothesis difficult to evaluate. Furthermore, Nicholson points out that vervet monkeys do not fit the cercopithecine pattern suggested by McKenna, as they display a great amount of non-aggressive allomaternal care.

Among primate species, alloparental behaviour can be performed by virtually all age/sex classes. Great interspecific differences exist, as do differences among researchers with respect to which types of behaviours constitute "alloparental" care. Suggested behaviours include allonursing, carrying of infants, protecting or removing infants from danger, grooming and nuzzling of

infants, providing reassuring contact, and play with infants by an older conspecific.

Gray (1985) suggests that alloparenting most likely serves varied functions in different species and cannot be explained by a single factor. Hinde (1974) speculates that marked inter-specific differences occur with respect to alloparenting as well as peer interaction because of inter-specific variation in terms of cost and benefit to both the mother and infant in relation to their interaction with conspecifics, as well as differences in cost and benefit to individuals other than the mother.

Theories concerning alloparenting by females and by males have been examined separately in reviews by Nicholson (1987), and Whitten (1987).

Females and Infants

Nicholson (1987) suggests that in the simplest terms, female/infant interactions can be divided into two main categories: affinitive and aggressive. She states that affinitive interactions can be viewed as allomaternal care, and those that are aggressive can be considered abusive. Nicholson feels that separating allomaternal care from abuse provides a framework within which to discuss functional interpretations of proposed female/infant interactions. She points out that alloparental care and behaviour can be influenced by infant's age, rank of the mother, degree of relatedness between infant and alloparent, and the age and maternal experience of the allomother.

Nicholson states that the existence of alloparenting creates a problem with respect to evolutionary theory, because allomaternal behaviour resembles patterns of maternal behaviour, yet alloparents are less closely related to the

infant than is the mother. Thus, one must ask what benefits relative to costs does an allomother gain from such behaviour, and how do both the mother and the infant benefit? From an evolutionary standpoint, Nicholson proposes that allomaternal care could have evolved through kin-selection if mothers and infants receive some benefit from care by related animals, or if the long term benefit gained by young nulliparous females from practising maternal care is greater than the cost to the infant. However, she cautions that these hypotheses have not been tested because of the difficulty of determining and assessing the actual costs and benefits of allomaternal care.

Males and Infants

Whitten (1987) proposes five categories of infant/male relationships, and suggests that within a given social group more than one category can apply. These are outlined below.

1. Intensive Caretaking- where the male spends much of his day involved in infant caretaking.

2. Affiliation - where the male spends part of his day affiliating with one or more specific infants.

3. Occasional Affiliation - where the male is occasionally involved in affiliative interactions with one or more infants, but such associations do not occur on a regular, predictable basis.

4. Tolerance - the male tolerates infants in close proximity to him but otherwise interacts very little with them.

5. Use and Abuse - the male uses the infant to benefit hmself at the risk of harming the infant.

In those male/infant relations determined to be *affiliative*, Whitten states that the average overall rate of interaction is low, but that, within specific male/infant pairs, the frequency of affiliation is much higher. She notes that in species showing male/infant affiliative relations, males have been observed to hold, cuddle, groom, nuzzle, and examine infants. Whitten states that males in these species tolerate the close proximity of infants, and infants are allowed to play around and on adult males. In groups where males display *occasional affiliation*, Whitten notes that often such males are indifferent, yet under particular circumstances, they engage in affiliative behaviours with specific infants. It has been suggested that associations between infants and males can be beneficial to the infant in terms of protection from agonistic or overzealous conspecifics, greater access to food if the male allows the infant to share his feeding site, advantages of a "social umbrella" offered by a high ranking male, and benefits in later life such as the possibility of inheriting rank, if the adult male is high ranking (Gouzoules, 1984; Whitten, 1987).

Whitten states that even in species where male/infant interaction is not common, a number of types of male/infant relationships can develop, and seem to be related to factors such as the relationship between the male and the mother, the male's relationship to other males, and the needs of the infants.

Perhaps the most obvious explanation of male/infant interaction in a multi-male multi- female group would be that of parental investment. However, Whitten (1987) suggests that most of the interaction between males and infants are not examples of parental investment. She states that males in multi-male/multi-female species often affiliate with infants who could biologically be their own; however, she notes, they are just as likely to affiliate with infants who

are not. Whitten argues that male caretaking behaviours occuring in multi-male species incur no cost to the male's future reproductive success, and suggests that proximity, huddling, and "babysitting" of infants require little energy expenditure. Gouzoules (1984) suggests that individual infants should take advantage of such low-cost care given by males. In multi-male species where seasonal breeding occurs, Whitten notes that male affiliative interactions with infants have been observed to cease at the beginning of the mating season. Whitten suggests that male affiliation with infants may enhance a male's mating success, and notes that a number of studies have demonstrated that male/infant affiliations are often accompanied by bonds between the mother and the male. She states that an affiliation with an infant may help the male to establish a relationship with the mother, or it may be an extension of an established male/female relationship. Whitten stresses that the available data on male/infant relationships suggests that male association with infants is more closely related to maintaining relationships with females, and enhancing reproductive success, than with parental investment, and can be viewed as an important aspect of male reproductive success.

Section Two

Lemur catta - General Information

The ringtailed lemur (*Lemur catta*) occupies southern and southwestern Madagascar (Jolly,1966; Tattersall, 1982). Jolly (1966) reports that *L. catta* troops are composed of between 12 and 24 adults and juveniles. Sussman (1977) states that the average size of troops he studied was 17.5 (range 15-20). Mean troop size in the present study was 17.3 before the birth season (range 16

to 19 in the three focal troops), and 23, including infants, at the end of the study (range 21-25).

A *Lemur catta* troop is organized around a core group consisting of adult females, their infants, younger juveniles, and sometimes the dominant male or males (Budnitz and Dainis, 1975; personal observation). Budnitz and Dainis report that females spend their entire lives in their natal troop, while male troop exchange prior to the breeding season is common. Noticable separate dominance hierarchies are reported for females and males (Jolly, 1966; Budnitz and Dainis, 1975; Sussman, 1977). Females are dominant over males and juveniles in all cases (Budnitz and Dainis, 1975).

Jolly (1966) and Sussman (1977) found home ranges of *L. catta* troops studied at Berenty in the 1960's to be approximately 6 hectares with no overlap; however, in a subsequent study of the same area in 1970, Jolly (1972) observed that considerable ranging changes had occurred. She states that *L. catta* troops went from spatial exclusivity of a range to overlapping (termed "time plan sharing" by Jolly), and from relatively homogeneous feeding formation to staggered feeding with subordinate males feeding last. Jolly suggests that the abovementioned changes may have been due to either increasing population density or an adaptive reaction to short term food shortages as a result of a particularly dry year. Budnitz and Dainis (1975) found that smaller home ranges occurred in richer environments. In my study, the mean home range size of the three focal troops was approximately 3.7 hectares (range= 3.06 to 4.18 hectares). Range overlap did occur among all three groups. My study was conducted in a smaller area of Berenty than the main reserve where Jolly and Sussman carried out their studies in the 1960's and

1970's (see "Study Site" below). Because part of this smaller 10 hectare reserve area had at one time served as an orchard, it was rich in fruit trees; thus, Budnitz and Dainis' (1975) finding of smaller ranges in richer environments would apply in the present case.

Jolly (1966) reports that *L. catta* troops use one part of their home range for 3 or 4 days, then switch to another part, utilizing all parts of their range within 10 days.

Jolly (1966) and Sussman (1974,1977) state that *L. catta* troops spend between 20%-30% of their day on the ground. Furthermore, Sussman (1974, 1977) estimates that 71% of *L. catta* troop travel was done terrestrially. With respect to their daily activity periods, Jolly (1966) found that *L.catta* troops begin to move, sun, and feed anytime between 0530 and 0800, depending on temperature and weather conditions. She noted that troops engage in 4-5 long progressions daily. *L. catta* sleep between 1200 and 1600h. during the hot season, and for a shorter period during cooler weather. Jolly observed that *L. catta* troops were sometimes moderately active throughout the night, although she states that she made too few nocturnal observations to conclude whether or not a habitual nocturnal activity rhythm exists.

L. catta usually breed at two and a half years of age (Jolly,1966). The birth season occurs in late August and early September (Jolly,1966; Sussman, 1977; personal observation).

Study Site

Berenty, a private wildlife reserve, is owned by the deHeaulme family of southern Madagascar and has existed as a protected area since the 1940's.

The reserve is situated in an area of gallery forest surrounded by sisal plantations on three sides and the Mandrare River. Four distinct kinds of vegetation are found at Berenty, including riverine forest (along the Mandrare River banks), open deciduous forest, brush and scrub, and subdesert "spiny" forest (Budnitz and Dainis, 1975). The reserve is composed of one large area (Malaza) which includes an area of 100 hectares, and four smaller parcels of forest. The present study was conducted in Reserve #3, a 10 hectare patch of riverine, open deciduous, and brush and scrub forest which is connected to the main Malaza forest by a narrow corridor near the river.

Much tourism now exists at Berenty in Malaza, but tourists did not venture into the study area, approximately 1.5 km. from the main tourist area.

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Chapter 2: The Social Development of Infant *Lemur catta*

The social development of infant primates has been the focus of numerous studies. (Berman,1982; Box, 1975; Cleveland and Snowdon, 1984; Hoff et. al, 1981; Lee, 1984; Nicholson, 1982; Rhine et. al, 1984). Nicholson (1982) suggests that the examination of such development and independence is an important field of inquiry because, she argues, succeeding as a primate adult is contingent upon knowing the rules of the social system, having allies, and knowing what to expect from conspecifics.

Although infant social development has been examined in detail in many anthropoid species, little information exists in the primatological literature with respect to the process of social development in prosimian primates. Jolly (1966) and Sussman (1977) have outlined general aspects of social development and the socialization process in *Lemur catta* and *Lemur fulvus rufus* , but thus far, quantitative studies of social development in *Lemuriformes* do not appear in the literature. The purpose of this chapter is to examine and describe social development in *Lemur catta* , a female-dominant, primarily terrestrial *Lemuridae* species, which live in large, cohesive social groups. The developmental process will be considered within the framework of the stages outlined below. Conflict between the mother and infant with respect to weaning from the nipple and from dorsal riding will be discussed. Whether or not an infant's sex or rank affects the extent or severity of parent-offspring conflict will also be considered. Sex and rank will be examined in terms of measures of dependence on and independence from the mother.

Fragaszy and Mitchell (1974) suggest that the critical mother-infant bond is formed during the first, or neo-natal period, and that such a bond, which

involves constant and continuous contact between the mother and infant, is important with respect to the infant's subsequent socialization experiences. Once the infant begins to develop cognitive and motor skills, Fragaszy and Mitchell suggest that the close emotional and biological attachment so predominant in the first stage of development no longer fulfills the infant's need for stimulation, and thus, it commences exploration of the "non-mother" environment (stage two), wherein it begins to recognize and respond appropriately to conspecifics. Fragaszy and Mitchell argue that at this stage, the infant voluntarily interacts with troop members other than the mother and can be regarded as a participatory member of the social group, although it is still largely dependent on the mother. When interaction with conspecifics becomes regular, Poirier (1972) suggests that the infant enters the "peer socialization" stage of development (stage three) which is marked by both the weaning process and diminishing infantile behaviour patterns. At this point infants tend to associate principally with peers, and sexual patterns, appeasement gestures, and aggressive behaviours begin to emerge (Fragaszy and Mitchell, 1974).

The abovementioned weaning process is often characterized by a period of turmoil between a mother and her infant. Parent/offspring or weaning conflict (Trivers, 1974) in primates has been observed in baboons (Altmann, 1980; Nicholson, 1982), langurs, (Hrdy, 1977), Japanese macaques (Collinge, 1987), owl monkeys (Dixson & Fleming,1981), and chimpanzees (Goodall, in Trivers, 1985), and manifests itself in the form of temper tantrums and regression to infantile behaviours on the part of the infant, and rejection and other forms of punishment on the part of the parent. Nicholson (1982) suggests that nursing is one of the most obvious forms of parental investment as defined by Trivers

(1974) and that infant carrying is also energetically costly, especially as the infant's weight increases. Thus, she suggests, the above behaviours are likely to become major sources of parent-offspring conflict during particular developmental stages.

With respect to sex differences in infant social development, various explanations have been offered to account for the presence or absence of such differences, in different species. For example, Nicholson (1977) suggests that environmental characteristics may influence the development of independence to different extents in male and female chimpanzee infants. On the other hand, Nash (1978) argues that differences in behavioural development in infant baboons may be ascribed more to individual circumstances than to sex of the infant.

Issues and questions to be addressed in this paper include:

1) At what age (week of life) specific behaviours and/or developmental markers such as time on and off the mother, time spent with the mother, distance from the mother, frequency and duration of maternal grooming, environmental exploration and play behaviour, and development of independent foraging and locomotion, were first observed, and how these correspond to the three developmental stages outlined above.

2) Whether or not sex or rank differences exist with respect to frequency of social and solitary play.

3) At what age adult behaviours performed in the context of play begin to emerge.

4) At what age infants begin to be subject to dominance relations by conspecifics, and what types of dominance behaviours are directed towards infants.

5) At what age dominance behaviours and agonistic signals directed *by* the infant *towards* conspecifics emerge.

6) During what week of life parent/offspring conflict in *Lemur catta* begins, how it is manifested, and whether the infant's sex or rank affects the frequency of maternal rejections from the nipple and from dorsal riding.

7) Is an infant's sex or rank reflected in measures of dependence and independence?

Methods

The study was carried out from July to the end of December, 1987 at the Berenty Reserve, southern Madagascar. Berenty is situated in an area of gallery forest surrounded by sisal plantations and the Mandrare River. The total area is approximately 100 hectares (Jolly,1972). The reserve is composed of 4 main types of vegetation: closed canopy, open forest (including thorny vines), brush and scrub forest, and subdesert or "spiny" forest (Budnitz and Dainis,1975) . The home ranges of the animals in the current study included the first three types of forest.

The average rainfall in the area is approximately 500 mm. per year, mostly falling between January and March, although some years there has been no rain at all (Budnitz and Dainis, 1975).

The five months of the study covered the period from a month before the beginning of infant births to the end of the sixteenth week of the infant's lives. A total of twelve infants (the first twelve born) from three different groups of *Lemur catta* were chosen as focal animals (for composition and census figures for each focal troop see Appendix 1) One of the infants died at the end of the second week of life and the data collected on this particular infant was not

included in the analysis. The remaining sample consisted of five female and six male infants. Infant's rank was based on rank of the mother. Rank of the mother was determined by observing the direction of agonistic signals directed towards the mother by other adult females, such as cuffing and supplanting, and submissive signals such as supplantation and submissive chattering, particularly at feeding, drinking, and rest areas. Exact birthdates of each focal infant are known. *Lemur catta* births are highly seasonal, with the majority occurring within a 2-3 week period between the end of August and mid-September. There was an eleven day separation between the births of the first and last of the focal infants.

Lemurs at Berenty Reserve are highly habituated to the presence of humans; thus, I was generally able to conduct focal animal observations between 2 and 5 meters from the focal troop. Binoculars were used when necessary.

Sampling was carried out during *L. catta's* active periods, between 06:30 or 07:00h (depending on the time of sunrise), and 09:30 or 10:00h, and again between 15:30 and 18:00. Data were collected using the continuous time focal animal sampling technique (Altmann,1974; Lehner, 1979) with a detailed ethogram (Appendix 2). Focal animal sessions were of 10 minutes duration. During each session all behaviours in which the subject engaged, all behaviours directed towards the subject, as well as exact times the behaviours occurred were recorded. Each focal group was followed for either an entire morning or afternoon, and the sequence of focal animal observations was randomized and determined at the beginning of each week of observation. An attempt was made to collect five sessions on each focal infant per week of life. A total of 260 hours of observation on the three *L. catta* groups was made, including 144 hours of focal animal sampling.

Results

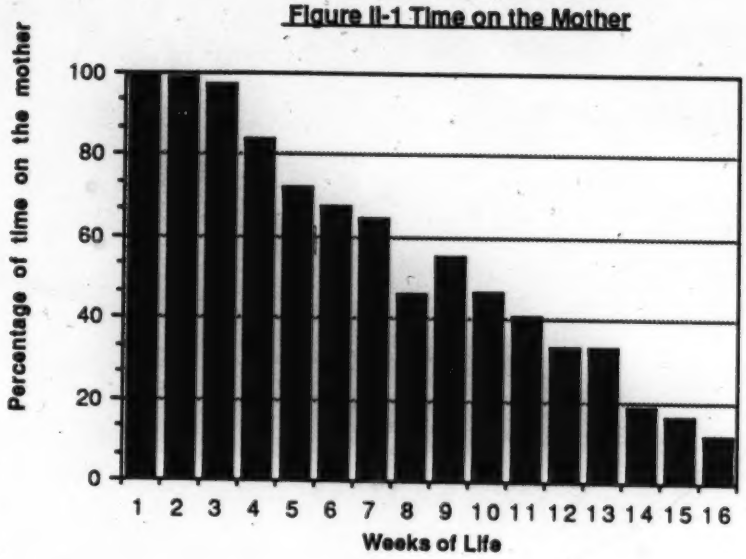
Behavioural Development in Stage One

Time on and off the Mother, Grooming by the Mother, and Distance from the Mother

A strong negative correlation exists between infant's age (measured in terms of weeks of life) and amount of time spent engaged in behaviours *on* the mother, such as ventral-ventral and ventro-dorsal carrying and sitting, suckling, test foraging while sitting on the mother, exploration of the mother, and observation and exploration of the environment while sitting on the mother ($r = -.98$, $p < 0.001$).

The decrease in time spent by infants on the mother is particularly noteworthy between weeks 3 and 4, with a decrease from 96.1% to 84.0%, weeks 4 and 5, with contact time decreasing from 84.0% to 72.0%., and between weeks 13 and 14 with a decrease from 33.4% to 18.8% (Figure II-1). These particular weeks coincide with what appear to be particular developmental markers. Between weeks 3 and 5, infants began to regularly leave their mothers to engage in exploration of the environment, and infants began making long terrestrial progressions on their own, and stopped running to the mother when group alarm calls were given, during weeks 12 and 13.

Figure II-1 Time on the Mother



Conversely, there is a strong positive relationship ($r=.96$, $p<0.001$) between infant's age and amount of time spent in behaviours related to independent exploration of the environment, such as locomotion, solitary locomotor play, exploratory play, sniffing and manipulating objects in the environment, independent foraging, and branch marking practice (the latter behaviour performed only by infant males from the 15th week of life).

Time spent with the Mother

A strong negative relationship was found between infant's age and time spent in activities *with* the mother, which include all of the abovementioned "on the mother" behaviours, as well as locomoting to and playing with the mother. ($r=-.96$, $p<0.001$).

Frequency and Duration of Maternal Grooming

A strong negative correlation exists between the frequency of maternal grooming and infant's age (weeks of life) ($r = -.87$, $p < 0.001$).

An equally strong negative correlation also exists between the duration of maternal grooming bouts and infant's age ($r = -.87$, $p < 0.001$).

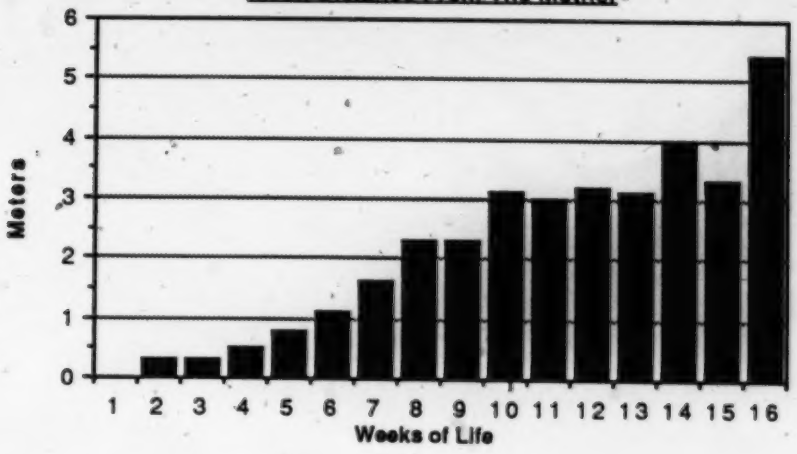
Behavioural Development in Stage Two

Distance from the Mother

Infant's distance from the mother was recorded when the infant was engaged in exploration of the environment. Between weeks three and four, environmental exploration consisted of locomotion between the mother and another conspecific, or the mother and an inanimate object such as a tree, bush, or log. After week four, infants began manipulating objects in the environment, hopping and leaping, climbing at low heights off the ground, and hanging from branches.

A strong positive correlation existed between infant's age and mean distance from mother in exploratory play ($r = .96$, $p < 0.001$), (Figure II-2).

Figure II-2
Mean Distance From The Mother



Infants were first observed engaging in environmental exploration off the mother in week 2. During the first few weeks, behaviours designated as environmental exploration included hopping a short distance from the mother (less than half a meter), and immediately hopping back and onto the mother's dorsum. After weeks 2 and 3, infants begin experimental climbing and jumping on low branches and logs, hanging by their feet from low branches, and making short leaps between close branches. By week 8, infants were able to run, leap, and hang with some skill high in the canopy.

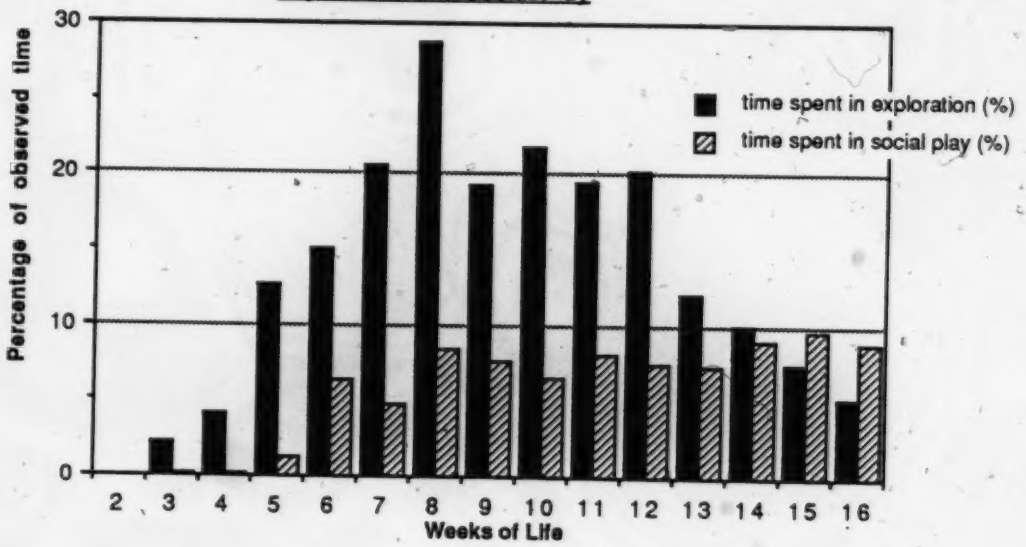
Environmental exploration peaked in weeks 7 and 8 then gradually dropped off until it comprised only 5.15% of the total sample time by week 16 (Figure II-3).

Behavioural Development in Stage Three

Social Play

Social play in infant *L. catta* consists of chasing, play-biting, jumping on, and wrestling with one or more play partners. The first instance of social play behaviour noted was an infant play-biting with its mother during the third week of life. The first time an infant was observed in social play with peers was during week 6. Baldwin (1986) states that play begins *after* exploration and develops *from* exploration. A comparison of environmental exploration with play behaviour is presented in Figure II-3 below.

Figure II- 3
Percentage of Observed Time Spent in Exploration and Social Play



Infants tended to spend much more of the observed time engaged in environmental exploration than in play. Time spent in play exceeded time spent in exploration for weeks 15 and 16 only.

Sex Differences in Play

No significant difference was found with respect to sex of the infant and frequency of social play bouts (Mann-Whitney U test, U=9, p>0.05). Female infants tended to play slightly more frequently (n=5, mean=5.4 +2.3SD play bouts per hour) than did male infants (n=6, mean=4.16 +1.3SD play bouts per hour), but the difference was not statistically significant.

Rank Differences in Play

Infants of middle ranking mothers in the sample had a slightly higher mean rate of play bouts per hour than did infants of high or low ranking mothers (middle ranking infants, n=3, mean=6.1, range=2.3-7.9 play bouts per hour, low ranking infants, n=3, mean=4.5, range=2.9-6.2 play bouts per hour, high ranking infants, n=5, mean=3.9, range=2.3-5.8 play bouts per hour).

Solitary Locomotor Play

Solitary locomotor play was characterized by very rapid terrestrial or arboreal running and leaping, twirling on branches, and hanging from thick branches by the feet. Slight differences with respect to sex were found, but these were not statistically significant (Mann Whitney U test, U=15, p>0.05). Female infants engaged in such play more frequently than did males (female mean rate of solitary play bouts per hour=0.6 +0.4SD, male mean=0.1 +0.2SD). Infants of

middle ranking mothers had higher mean rates per hour than infants of either high or low ranking mothers (mean rate per hour for infants of middle ranking mothers=0.7, range=0.4-1.2, infants of high ranking mothers=0.1, range=0.0-0.5, infants of low ranking mothers=0.4, range=0.0-0.8).

Adult Behaviours in Infant Play

In the study sample, infant males began "mock" stink fighting and branch marking during weeks 14 and 15. Subadult and adult male *L. catta* habitually palmar mark and wrist spur mark tree trunks and branches (Jolly, 1966). Sussman (1977) notes that he observed an infant attempt such behaviour between 2 and a half and 3 months. At 14 weeks of age, male *L. catta* infants have no wrist spur; nevertheless, marking behaviour was observed 3 times in weeks 14 and 15. Infants attempted to mark branches, small twigs, and even grass stalks. Anogenital marking of physical objects in the home range, a common female territorial defense behaviour, was not observed in female infants during the study period.

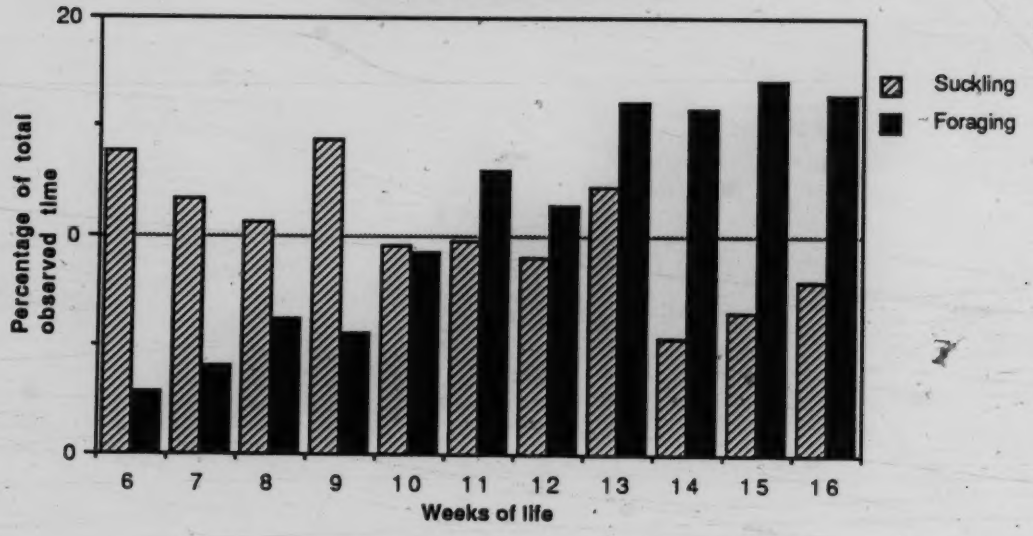
"Stink fighting" is a typical male agonistic behaviour in *L. catta* wherein the tail is pulled between the forearms and impregnated with scent from the bracheal gland and then waved above the head towards the opponent. Such behaviour is performed by adult males, primarily during mating season (Jolly, 1966). Infant males in the focal sample were observed performing the gestures of "stink fighting" in the context of play, in week 14. Such behaviour was noted to occur 10 times during the last 2 weeks of the study.

Development of Independent Foraging and Locomotion

Infants were noted to begin ingesting solids at 6 weeks. A few weeks prior to actual foraging, infants were observed nibbling on shoots, buds, leaves and fruits, but at this age they rarely ingested the tested food item.

Foraging increases steadily with infant's age (Figure II-4). Between weeks 13 and 16, the amount of time infants spent in foraging levels off. During the last 4 weeks of the study, infants were observed to spend an average of 16% of their total time engaged in foraging activities. Infants reduce their time on the nipple by nearly 7% between weeks 13 and 14, and the amount of time spent suckling levels off for the remainder of the study. It should be noted, however, that at 16 weeks of age, *L. catta* infants are still spending a relatively large amount of observed total time on the nipple.

Figure II-4
Percentage of time
spent suckling and foraging



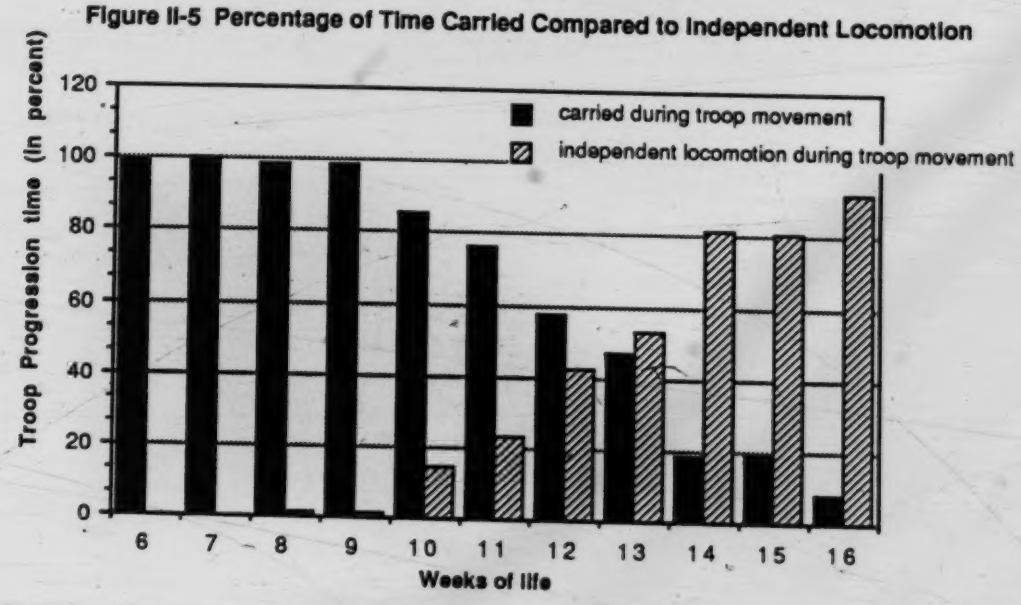
Development of Independent Locomotion in Troop Movement

Infants begin locomoting independently during short-distance troop travel in week 6, but only very briefly before resorting to dorsal riding. By week 8, they regularly followed their mothers short distances, but continued to ride during long arboreal or terrestrial progressions. Independent locomotion during long-distance troop travel occurred initially two weeks earlier for arboreal than for terrestrial progressions. The first independent arboreal progression was observed during week 12, and the first long distance terrestrial travel in week 14.

Independent locomotion of infants during troop movement in week 10 is markedly increased over that of week 9 (14.4% of total troop movement time for

week 10, compared to 1.4% for week 9) (Figure II-5). Comparisons between weeks 11 and 12, and weeks 13 and 14 also show much greater increases.

Figure II-5 Percentage of Time Carried Compared to Independent Locomotion



Dominance and Agonistic Behaviours

Dominance Behaviours Directed Towards the Infant

Infants began to be subject to dominance relations by conspecifics in the sixth week of life. The first observed instance of such behaviour occurred when a 6 week-old female infant was cuffed by another mother. Displays of dominance (in the form of cuffing) were directed most frequently to infants by other mothers (n=13, weeks 6 to 16), followed by mothers (n=2, weeks 6 to 16). Subadult females were observed to cuff infants twice (weeks 9 and 16). Only one instance of supplantation was observed, directed by another mother towards a

male infant of a lower ranking mother. Dominance behaviours directed towards infants were not observed to occur from animals of any other age/sex class.

Infants rank did not appear to be a factor in the frequency of agonistic behaviours directed towards them. Infants of high, middle, and low ranking mothers were the recipients of agonistic behaviour relatively equally. For example, infants of high ranking mothers (n=5) were observed to receive cuffs 8 times during the course of the study, and infants of middle (n=3) and low (n=3) ranking mothers both 6 times.

Only once during the study did I observe an infant being attacked by another mother. This occurred during an inter-troop confrontation and the attacker was from the other troop.

On two occasions in one of the focal troops, two low ranking mothers were prevented from retrieving their infants, who were displaying signs of distress (emitting lost calls). On both occasions, higher ranking females and juveniles surrounded the infant and groomed it while it cried, but whenever the mother attempted to approach the infant she was chased by one or more dominant females. The above situation was never observed in the other two focal troops.

Dominance and Agonistic Behaviours Directed By the Infant Towards Conspecifics

Infants were observed to begin displaying dominance behaviours such as cuffing and supplanting in week 15, although the frequency of such behaviours was very low. Only once was supplantation observed, by a 15 week old female infant to an infant male of the same age. Infant males were seen to cuff other infant males a total of 3 times during the 15th week of life. Fights between infants were noted nine times during the study, beginning in week 12. Eight of

these were initiated by infant females. Such behaviour consisted of squealing and very rapid biting,cuffing, and kicking. Fights usually occurred on a tree branch and always ended by one or both infants falling to the ground. Often the infants' mothers as well as other adult females would immediately appear at the scene of a fight. A breakdown of instances of observed fighting behaviour is presented below.

-infant female with infant male: four times, weeks 12,13 and 15.

-infant female with infant female: twice, weeks 15 and 16.

-infant female with infant,sex unknown: twice, weeks 14 and 15

-infant male with infant, sex unknown: once, week 12.

Weaning and Parent/Offspring Conflict

Triver's theory of parent/offspring conflict, discussed in the introductory chapter, was examined in the present study.

Weaning from the nipple was observed to begin in week 8. Rejection from dorsal riding began in week 12. It was found that age of the infant positively affects the number of maternal rejections from the nipple, from dorsal riding, as well as from "other" types of rejections by the mother, which included rejection from infant's attempts to approach, groom and sit beside the mother during the weaning period ($r=.75$, $p<0.001$).

Rejections from the nipple and from dorsal riding were also considered individually. The strongest correlation occurred between age and rejection of dorsal sitting and riding ($r=.74$, $p<0.001$, total number of observed dorsal rejections=56), followed by age and rejection from the nipple ($r=.64$. $p<0.01$, observed nipple rejections=69).

Figures II-6 and II-7 illustrate mean rejections per session on a week by week basis beginning with the onset of rejections (week 8 for nipple rejections, week 11 for rejections form dorsal riding).

Figure II-6 Rejections from the Nipple

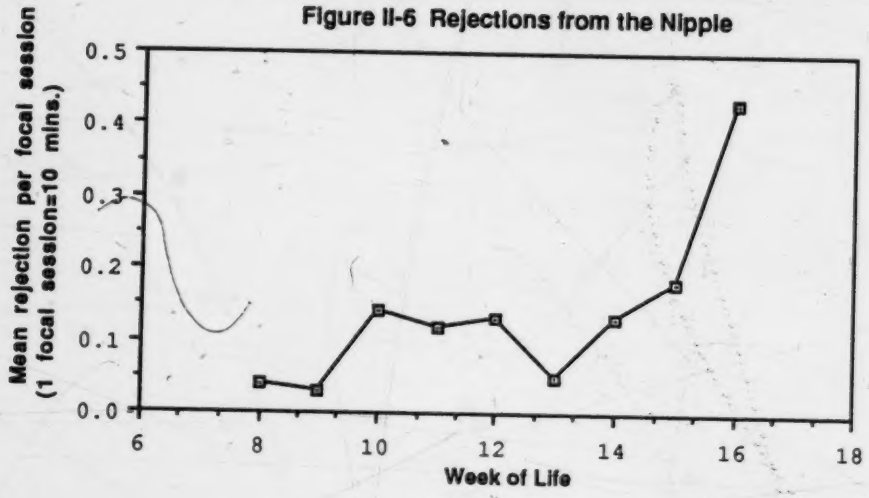
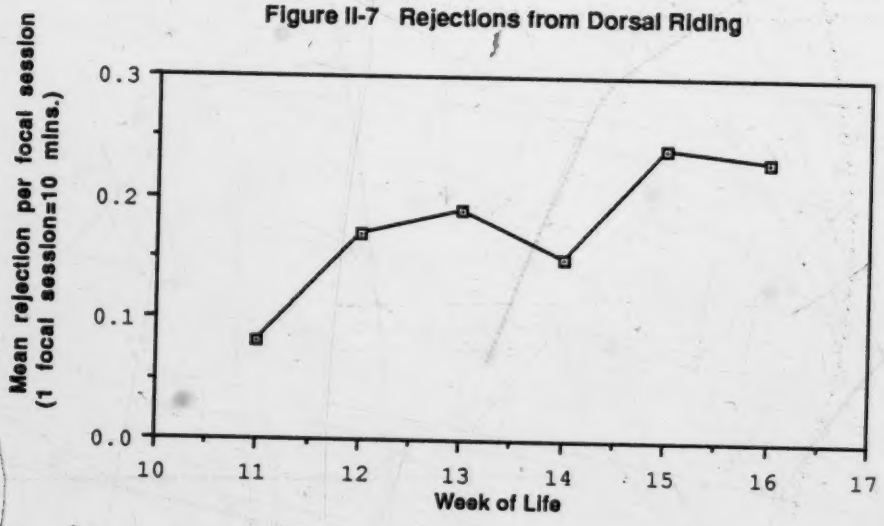


Figure II-7 Rejections from Dorsal Riding



Infant Sex and Weaning

Significant differences were not found in terms of frequency of rejection and infant's sex (Mann-Whitney U-test, $U=14$, $p>0.05$). Male infants were rejected only slightly less often than were female infants (mean overall freq.= 0.9 for males, and 1.1 for females).

Infant Rank and Weaning

No significant difference was found with respect to frequency of rejection and infant's rank (Mann-Whitney U test, $U=12$, $p>0.05$). Infant's rank was based on rank of the mother, which was determined at the beginning of the study (see Methods) During the period in which infants were still largely dependent upon the mother, they appeared to be treated in a similar manner to the mother with respect to agonistic and submissive signals.

Behaviours Related to Rejection From the Nipple and from Dorsal Riding

Rejection of infants from the nipple by mothers included behaviours such as nipping, cuffing, and pushing the infant when it attempted to suckle. More subtle approaches consisted of mothers raising their arms or lying on the stomach to prevent access to the nipple.

Infant strategies for gaining access to the nipple included grooming the mother until the infant's head was grooming the breast area, and dropping or pushing the head under the mothers arm while dorsal sitting or riding.

Behaviours performed by the mother to prevent dorsal sitting and riding ranged from mothers turning and cuffing or biting infants when they attempted to dorsal sit, to mothers standing up bipedally and shaking the infant off the

back or rolling on the ground, thereby forcing the infant to fall off. The latter two behaviours appeared much more severe than the former and always involved much squealing on the part of the infant, and often vocalizing on the part of the mother.

21.8% of rejections from dorsal sitting and riding were followed by vigorous grooming of the mothers by their infants. Such grooming differed qualitatively from infant grooming of conspecifics in relaxed social situations, in that the grooming movements in the rejection situation were larger, exaggerated, and very quick. The duration of such grooming bouts was never longer than a few seconds.

Measures of Dependence and Independence and Sex and Rank of Infant

Measures of dependence were based on the frequency of behaviours such as riding and sitting on the mother, following the mother, rates of seeking the nipple and suckling, foraging, observing and exploring the environment while sitting on the mother, emitting lost call vocalizations, and searching for the mother. Infants of lower ranking mothers displayed such behaviours significantly more frequently than those of high ranking mothers (Mann-Whitney U-test, $U=0$, $p<0.05$). However, no significant difference was found with respect to measures of dependence and sex of the infant (Mann Whitney U test, $U=11$, $p>0.05$)

Measures of independence were based on the frequency of the following behaviours: exploration of the environment, independent locomotion, arboreal and terrestrial progressions, independent foraging and drinking at the water

source (off the mother), grooming to conspecifics, mutual grooming, and playing with conspecifics.

No significant differences were found for the above measures and infants sex (Mann-Whitney U test, U=14, p>0.05), or rank of infant (Mann-Whitney U test, U=9, p>0.05).

Discussion

Stages of Development

The first 16 weeks of an infant *Lemur catta's* life is characterized by a period of rapid physical and social development in relation to most anthropoid species (Table II-1). Behavioural changes noted during this period cover the three general stages of primate infant social development suggested by Poirier (1972) and Fragaszy and Mitchell (1974).

Table II-1 Comparison of Some Developmental Markers in Lemur catta, Lemur fulvus rufus, Aotus trivigatus,Papio cynocephalus, and Gorilla gorilla gorilla

	Lc.[1]	*Lf.r.*[2]	*At*[3]	*Pc.*[4]	*Ggg*[5]
transition from ventral to dorsal carrying	2 wks.	1 mo.	—	4-6mos.	3-4 mos.
transition from riding to walking	10-12 wks.	13-16 wks.	18 wks	6 mos.	3-4 mos.
environmental exploration and peer interaction	3-4 wks.	8 wks.	—	4-6 mos.	8 mos.
maintaining distance from mother (or primary caregiver) for long periods	10-12 wks.	11-12 wks.	18 wks.	7-6 mos.	15-18 mos.
subject to dominance relations by conspecifics	14 wks.	—	—	4-6 mos.	—

Sources
1 personal observation
2 Sussman (1977)
3 Dixson and Fleming (1981)
4 Rhine et al. (1984)
5 Hoff et al.(1981)

The first, or neo-natal stage, characterized by constant mother/infant contact (Poirier, 1972), is of extremely short duration in *Lemur catta* , as infants were observed to begin exploration of the environment, which has been suggested to be a behavioural marker of the second developmental stage, between the second and third week of life. Strong negative correlations were found with

respect to age and time spent *on* the mother, age and time spent *with* the mother, and both frequency and duration of maternal grooming. Nicholson (1982) states that to become socially independent, an infant must move physically apart from the mother so that interaction with others can take place. In the present study, a strong positive relationship was found between infant's age and distance from the mother. Baldwin (1986) argues that environmental exploration and play are among the more important behaviours which broaden the infant's experience and facilitate its behavioural development. He suggests that benefits of environmental exploration include physical exercise, stimulation and development of the nervous system,development of perceptual and motor skills, coordination, development of predator defense skills, and generally overcoming helplessness by developing competence in the environment. A strong positive correlation was found in the sample between infant's age and amount of time spent in environmental exploration. Exploration peaked in weeks 7 and 8, then gradually levelled off until it comprised only 5% of the total sample time by week 16. During the peak period, infants spent more time suckling than they did foraging, and were carried far more than they walked during troop travel. I suggest then, that since a great amount of energy was *not* expended in either foraging or independent locomotion during the weeks when environmental exploration peaked, infants presumably had greater amounts of energy and time available to engage in such developmentally important behaviours.

Play

Both Poirier (1972) and Baldwin (1986) emphasize the importance of play behaviour in social development. Poirier suggests that play helps the infant adjust to the social milieu of the group, and that through the continual repetition of play behaviours, an infant learns the limits of its self-assertive capabilities. Baldwin notes that social skills which develop from play include the development of social bonds, cooperative relations, social perception, sex roles, and parental and communication skills.

Sex differences in social play were not found in the sample. Female infants tended to have higher frequencies of social (rough and tumble) play bouts than did males; however, the difference was not statistically significant. The above result differs from many studies of anthropoid primate infants, in which male infants have been found to engage in significantly more rough and tumble play than female infants (Baldwin, 1969; Nicholson, 1982; Lee,1984). Perhaps the lack of sex differences in the amount of social play in infant *Lemur catta* can be attributed to female dominance in this species ie: adult females engage in territorial defense which involve physical battles (Jolly,1966; personal observation). Adult males engage in physical fights during the mating season (Jolly,1966).If play is viewed as an opportunity for young animals to acquire, practise, and perfect skills which will be useful as adults in both social and agonsitic contexts, both adult female and male *L. catta* must develop skills which can be put to use in physical defense. Sex differences were not found in terms of sex and solitary locomotor play either. Rank of the infant did not have a significant effect on frequency of play. Middle ranking infants showed slightly higher mean frequencies of both social and solitary locomotor play.

Adult patterns such as copulatory behaviour and threat displays have been observed in play among infant marmosets (Box, 1975), and baboons (Rhine et. al,1984). Among infant *Lemur catta* males, attempts at brachial branch marking and "stink" fighting, which are considered territorial defense and threat behaviours in adult males, were observed in the context of play from week 14 onwards.

A much weaker positive relationship was found between infant's age and time spent with conspecifics other than the mother, than the strong negative relationship found between age and time spent with the mother. It appears then, that as infants mature, they balance their time and energy spent in social activites with that spent in necessary solitary self-maintainence activities such as foraging, self-grooming, and resting.

Development of Independent Feeding

Infant *L. catta* at Berenty are born near the end of the cooler dry season when food resources are relatively scarce. However, by the time they begin independent self-feeding around 6 weeks of age, resources have become much more abundant and it is thus possible for infants to benefit from new food items while at the same time continuing, for several more weeks, to benefit from nutrients found in the mother's milk that would not be found in weanling foods. This observation fits with Nicholson's (1982) proposal that suckling and independent feeding are complementary strategies to the infant primate. She suggests that since both adult and immatures share the same feeding area, infants are able to switch back and forth between suckling and foraging and thus are able to benefit simultaneously from both types of nutritional resources without experiencing an abrupt exchange of one feeding strategy for another. By the end of the 16th week of life, food items were varied and plentiful, and

suckling comprised only 8% of their total observed time, while twice that amount of time (16%) was taken up in independent foraging. From the onset of independent self-feeding to the end of the 16th week of life, both the decrease in suckling time and the increase in foraging time are steady and gradual.

Development of Independent Locomotion

Rhine et al. (1984) found that among free-ranging yellow baboons (*Papio cynocephalus*), the transition from riding to walking was at its peak around the 6th month (Table 1) , and that by one year, infants rarely rode on the mother. The authors state that once infants locomoted independently, regression to dorsal riding occurred infrequently and primarily only in dangerous situations. Dixson and Fleming (1981) note that infant owl monkeys (*Aotus trivigatus*) locomoted independently by 18 weeks of age (Table 1), and again, returned to the father to be carried only if a disturbance occurred.

Although infant *L. catta* in the study sample were observed to begin independent locomotion in week 6, it was not until week 9 that a sudden sharp peak occurred in terms of independent walking during troop travel (from 1.4% in week 8 to 14.4% in week 9). From week 9 onwards, the percentage of time during progressions increased steadily until in week 16, infants were locomoting almost entirely independently (92.1% of troop travel time). By the end of the study, infants were allowed to dorsal ride only in alarming situations or during excessively rapid terrestrial progressions, such as when one troop was being chased by another. This latter observation is similar to Rhine et al. (1984) and Dixson and Fleming's (1981) findings in yellow baboons and owl monkeys. Sussman (1977) suggests that the locomotor precociality of *L. catta* infants (Table 1) might be explained in terms of the energetic cost to the mother

of carrying a large and heavy infant on long terrestrial progressions, as well as the danger to both mother and infant if speed is limited by infant carrying and a dangerous situation should arise.

Infants and Dominance Relations

Infants at 6 weeks began to be subject to displacement and agonistic behaviours, although the overall frequency of such behaviours directed towards infants was low. All agonsitic behaviours directed *by* subadult and adults *towards* infants were performed by females. Again this might be explained by female dominance in *Lemur catta*, as Budnitz and Dainis (1975) note that females are dominant over males and juveniles in all cases. Even though infants from 6 to 16 weeks are growing increasingly independent, they can still, at times, be considered part of a mother/infant dyadic social unit, and that might explain the absence of agonistic gestures towards an infant by males.

Weaning and Riding Conflict

The first instance of weaning from the nipple was observed in week 8, from dorsal riding in week 12. The strongest positive relationship between age and rejection occurred with respect to dorsal riding. Age and nipple weaning had a slightly lower positive correlation. Rejections from dorsal riding were much more severe than those from the nipple. Nicholson (1982) states that the energetic cost to the mother of carrying an infant increases in direct proportion to its weight. However, she suggests that infant locomotion is also energetically expensive. Thus, Nicholson argues that it is very likely that infant carrying by the mother will be a major source of parent/offspring conflict during certain stages of infant development, particularly in primarily terrestrial species which

engage in long distance troop travel. *L. catta* are a highly terrestrial prosimian, spending more than 30% of their time on the ground (Sussman, 1977). I suggest,then, that the proximal expense to the mother in terms of infant carrying is greater than the proximal expense of nursing in the later stages of both types of weaning, since infants in the later weeks appeared to be at least half the size of the mother. This may explain why more severe conflict was found with respect to rejection from dorsal riding than rejection from the nipple.

Nicholson (1982) also noted that among baboons, infant grooming of the mother did not appear to be a significant aspect of weaning interactions. *Lemur catta* infants were observed to groom their mothers after a dorsal rejection 21.8% of the time, and the grooming itself was much more vigourous and exaggerated than grooming in a relaxed social context. Thus, I suggest that among infant ringtail lemurs, grooming to the mother in the context of rejection can be seen as an appeasement gesture and a notable aspect of weaning behaviour.

Much variability has been found with respect to rank and sex differences and weaning among anthropoid species. Lee (1984) found that female vervet infants tended to be rejected from nipple contact earlier than were males, and higher ranking mothers rejected their daughters more frequently than did low ranking mothers in the earlier stages of weaning. Berman (1984) notes that among rhesus macaques, mothers tended to reject male infants more frequently than female infants. Nicholson (1982) found no consistent rank related differences with respect to maternal aggression during weaning among free-ranging baboons; however, male infants were carried more frequently than were females. In my study, female infants were rejected slightly more often

than were male infants, but the difference was not significant. No differences were found in terms of rejection and mother's rank.

Measures of Dependence and Independence

Sex differences with respect to behaviours categorized as measures of independence were not found in the sample. Low ranking infants, however, demonstrated significantly higher frequencies of behaviours determined to be measures of dependence. One explanation for this finding could be that infants of low ranking mothers may not be as likely to be rescued by another troop member if a dangerous situation occurred and the infant was not in close proximity to its mother, since a high ranking female, by virtue of her position within the social group, may have more allies than a less dominant female. It appears as though the possibility of physical abuse of lower ranking infants by higher ranking group members can be ruled out in this case, as there was no evidence in the present study that low ranking infants received a greater proportion of aggressive behaviours than did high ranking young. However, the situation described on page 36, wherein a low ranking mother was prevented from retrieving her distressed infant by higher ranking females, might be considered a subtle form of agonistic behaviour directed towards a low ranking infant. An infant in such a situation could be more vulnerable to predators or injury if it is not permitted to reach its mother in a critical moment. Although this occurrence was only observed twice during the study, and in only one focal group, it may well occur in other groups. If so, this could serve as a factor in explaining the greater frequency of dependent behaviour among infants of low ranking mothers.

Conclusions

To summarize, the present study revealed the following:

1. By 16 weeks of age, infant *L. catta* were nearly independent of their mothers. Some suckling and dorsal riding still occasionally occurred, but at that age infants were manifesting many juvenile characteristics such as independent foraging, independent locomotion during troop progressions, being subject to dominance relations, and displaying some adult sex-specific behaviours.

2. The lack of sex differences in play found in this study may be related to the fact that as adults, both female and male *L. catta* engage in physical defense, and skills related to such defense may be acquired and practised in the context of social, rough and tumble play

3.Rank was not found to affect frequency or type of play behaviour.

4. Female infants were rejected slightly more frequently than were male infants; however, since the difference was not statistically significant it cannot be suggested as a trend.

5. Rank had no effect on the number of maternal rejections.

6. Parent/offspring conflict appeared to be more severe with respect to weaning from dorsal riding than weaning from the nipple.. This might occur because carrying a large, heavy infant on a long troop progression probably incurs a much greater immediate energetic cost to the mother than does a suckling bout.

7. Sex or rank differences were not found with respect to frequency of behaviours determined as measures of independence. Such behaviours are generally not performed in close proximity to the mother and are not dependent on the presence of the mother. A significant difference was found, however, in

terms of rank and measures of dependence. Behaviours included in this category occur either in physical contact, in close proximity, or, as in the case of lost calls, in pursuit of the mother. This finding could be related to the notion that lower ranking infants may need to maintain closer proximity to their mothers for a longer period of their early life than a higher ranking infant, because lower ranking young may not be as readily rescued in a stressful or dangerous situation by conspecifics other than the mother. Sex differences were not found in this category.

To conclude, *Lemur catta* is but one of approximately 36 species of prosimians (not including *Tarsiformes*). Further studies of infant ontogeny and social development in prosimians are needed both for comparison to the anthropoid species, and in order to achieve a better understanding of the developmental process in precocial prosimian primates, particularly in non-provisioned, field situations.

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Chapter 3: Alloparental Care and Affiliative Interaction with Infants by Conspecifics Other Than the Mother in *Lemur catta*

Alloparenting, or infant care performed by group members other than the mother, has been reported for many primate species (Rhine and Hendy-Neely, 1978; McKenna, 1979; Dixson et al, 1981; Zucker and Kaplan, 1981; Berman, 1982; Nishida, 1983; Cleveland and Snowdon, 1984). All age/sex classes have been noted to engage in alloparental care, and marked interspecific differences exist as to which individuals or classes provide such care. Alloparenting most likely serves varied functions in different species and cannot be explained by a single factor (Gray 1985). Hinde (1974) suggests that marked differences between species occur with respect to alloparenting because of interspecific variation regarding costs and benefits to the mother and infant in relation to their interaction with conspecifics, and also variation in cost and benefit to other group members.

In her 1966 pioneering study of *Lemur catta* social organization and behaviour, Jolly briefly discusses some aspects of alloparenting in the species, but to date, a detailed examination of this phenomenon has not been undertaken for any of the Lemuriform species. The purpose of this chapter is to investigate which group members, in terms of age/sex class, performed alloparental care and engaged in affiliative interactions with infants, as well as to suggest what the adaptive significance of such behaviours might be (ie: how particular individuals might benefit). A breakdown of types and amount of alloparental care observed during the 16 week study is presented with respect to frequency, duration, age/sex class of the animal performing the care, and

rank of the infant receiving such care. Whether or not the patterns observed in the present study fit with the existing explanations of costs and benefits of alloparental care, as well as suggestions for the adaptive significance of such behaviour, will also be discussed.

Numerous explanations have emerged regarding the adaptive significance of alloparental care. The beneficiaries of such care are variable, depending upon the species and the type of alloparental care observed. For example, the "mother relief" explanation suggests that the mother receives the greatest benefit, because by allowing others to care for and spend time with her infant, she gains free time to forage or rest (Gray, 1985). The most common explanation appears to be that of "learning to mother" (Lancaster, 1971; Hinde, 1974; Hrdy, 1976; Nishida, 1983; Gray, 1985). In this case it is young, nulliparous females who benefit most by gaining maternal experience through allomothering before giving birth themselves. Young females in many species have been found to perform a relatively greater amount of care than their conspecifics of other age/sex classes (Nicholson, 1987). Indeed, Nicholson suggests that allomothering may have a specific developmental function in young nulliparous female primates. If an infant receives alloparental care exclusively or almost exclusively from one particular individual, the infant could benefit by being adopted by that individual if the natural mother should die (Nishida, 1983; Gray, 1985). Furthermore, if an infant is kidnapped by a higher ranking, lactating female, Hrdy (1976) suggests that both the natural mother and the infant benefit, because in such a case, the natural mother is free to resume cycling and thus, she may be in a position to enhance her reproductive success, and the infant experiences an increase in status. Lower ranking allomothers might benefit if they are able to form an alliance with a higher ranking female by

caring for her offspring (Nishida, 1983; Gray, 1985). Through such an alliance, a lower ranking female could gain better access to resources, such as preferred foraging sites and sleeping areas. Furthermore, if rank is found to correlate positively with amount of alloparental care, a female whose rank increases as a result of alloparenting could eventually benefit once she herself reproduces. In a species where the female dominance hierarchy is of great importance with respect to resource competition, an allomother could reduce such competition for herself and her offspring if she is able to lower the inclusive fitness of another infant and its kin by abusing or caring poorly for another infant (Gray, 1985).

Issues and questions to be examined in this paper include:

1) Whether or not differences exist in terms of the frequency and duration of alloparental care directed towards infants with respect to age/sex class of the alloparent. If such differences exist, which of the proposed explanations for alloparental care (outlined above) can be applied to the situation?

2) Whether relationships exist between specific types of alloparental care and/or infant-conspecific interactions, and age/sex class of the alloparent. If so, how can such relationships be explained as adaptive?

3) Whether or not adult male *Lemur catta* engage in alloparental care of and/or affiliative interactions with infants, and if so, what might be the adaptive significance of such care and interaction for both the male and the infant?

4) Whether infants of high-ranking mothers receive more alloparental care than those of low ranking mothers.

Methods

The present study of alloparental care among *Lemur catta* was part of a larger study of infant social development in this species. Research was conducted between July and the end of December, 1987, at the Berenty Reserve, southern Madagascar. Berenty is situated in an area of gallery forest surrounded by sisal plantations and the Mandrare River. The total area is approximately 100 hectares (Jolly,1972). The present study was carried out in a 10 hectare area of the reserve which encompassed the complete home ranges of the three focal troops. Four primary types of vegetation occur in the reserve: closed canopy, open forest (including thorny vines), brush and scrub forest, and subdesert or "spiny" forest (Budnitz and Dainis,1975) . The home ranges of the animals in the current study included the first three types of forest.

Little rainfall is reported to occur in the area of Berenty. The average is estimated at 500 mm. per year, falling primarily between January and March. During some years no rainfall at all has been recorded (Budnitz and Dainis, 1975).

The five months of the study covered the period from a month before the beginning of infant births, when censusing of *L. catta* troops was performed and home ranges of chosen focal troops were determined, to the end of the sixteenth week of the infant's lives. Initially 12 focal infants were chosen; however, one died at the end of its second week of life. Data on this particular infant was excluded from the analysis. Five females and six males constituted the remaining sample. Exact birthdates of each focal infant is known. *Lemur catta* births are highly seasonal, with the majority occurring within a 2-3 week period between the end of August and mid-September. There was an eleven day separation between the births of the first and last of the focal infants.

As *Lemur catta* at Berenty are highly habituated to human presence, it was possible to conduct focal animal observations from between 2 and 5 meters of the troop. Binoculars were used when necessary.

Sampling was carried out during active periods for *L. catta* , between 6:30 or 7:00 am (depending on the time of sunrise), and 9:30 or 10:00 am, and again between 15:30 and 18:00. Continuous time focal animal sampling was used as the data collection method (Altmann,1974; Lehner, 1979), with a detailed ethogram. Focal animal sessions were of 10 minutes duration. During each session all behaviours in which the subject engaged, all behaviours directed towards the subject by conspecifics, as well as the exact times when the behaviours occurred were recorded. Thus, determination of durations and frequencies of all behaviours and interactions (including alloparental care) was possible. I was able to record the age/sex class of the alloparent 85% of the time. Each focal group was followed for either an entire morning or afternoon, and the sequence of focal animal observations was randomized and determined at the beginning of each week of observation. An attempt was made to collect five sessions on each focal infant per week of life. A total of 260 hours of observation on the three *L. catta* groups was made, including 144 hours of focal animal sampling. Because focal animal data were collected on the infants in order to evaluate social development, and not the conspecifics performing the alloparental care, it was not possible during the data analysis to determine variation between individual alloparents of particular age/sex classes; thus, tests of analysis of variance were not possible, and statistical analysis for this part of the study consisted of Chi-square goodness of fit tests and Mann-Whitney U-test.

Differences occur among researchers in terms of which behaviours constitute "alloparental care". Suggested behaviours generally include allonursing, carrying of infants, protecting or removing infants from danger, grooming and nuzzling of infants, providing reassuring contact, and play with infants by an older conspecific. However, these are highly variable depending upon the species or study, as different species exhibit different behaviours which can be classified as "alloparental care". Some of the abovementioned behaviours, such as providing reassuring contact and social play with infants might be classified as "interactive" but not "alloparental"; however, all of the above have been included in studies of alloparenting. For the purposes of my study, which looks at both infant care by conspecifics other than the mother, and infant-conspecific interaction, behaviours which I considered alloparental included carrying and grooming of infants, allonursing, and social play with infants performed by conspecifics of older age/sex classes. Mutual grooming *with* infants was considered an affiliative, socialization behaviour, but not an alloparental one (see Ethogram, Appendix one).

Results

Differences in Frequency and Duration of Alloparental Care According to Age/Sex Class of the Alloparent

Frequency of All Alloparental and Affiliative Behaviours

When all alloparental and affiliative behaviours were examined together, a significant difference was found with respect to the frequency of alloparenting and affiliative interaction according to the age/sex class performing the behaviour (Table III-1).

Table III-1: Frequency of All Alloparental and Affiliative Behaviours

Age/Sex class	Observed mean frequency	Expected mean frequency	O-E	$\frac{(O-E)2}{E}$
Other mothers	23.2	23.1	0.1	0.0
Adult females without infants	26.0	6.1	19.9	64.9
Young females	15.1	12.3	2.8	0.6
Young males	9.8	13.8	-4.0	1.1
Adult males	4.5	23.1	-18.6	14.9

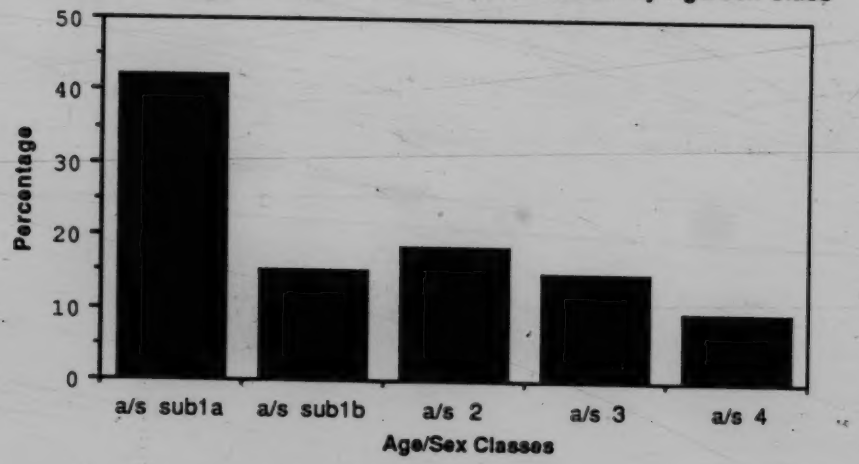
$\chi 2 = 81.5$, d.f.=4, $p<0.001$

The greatest differences from the expected frequencies occur with respect to adult females without infants and adult males as indicated in the column "O-E" (19.9 for adult females without infants, and -18.6 for adult males). Alloparental behaviours were performed most often by both adult females without infants and other mothers, followed by young females, young males, and finally adult males. "Young" females and males refer to yearling animals (juveniles), and 2 year olds (sub-adults). Young animal age classes were determined by the size and color of the genitalia, and in the case of males, whether or not the testes had descended, and scrotum size.

With respect to amount of time of alloparenting activities received by infants, other mothers contributed the most time (total observed duration in seconds) to alloparental care (42.2% of the total time spent in alloparental behaviour where it was possible to determine age/sex class. Total observed time group members

spent in alloparental care= 8 hours). Young females contributed to 18% of the total time, followed by adult females without infants (15%), young males (14.%), and adult males (9%) (Figure III-1).

Figure III-1 Percentage of Total Alloparental Care by Age/Sex Class



Age/Sex sub-class 1a= Other mothers
Age/Sex sub-class 1b= Adult females without infants
Age/Sex class 2= Young females (juveniles and sub-adults)
Age/Sex class 3= Young males (Juveniles and sub-adults)
Age/Sex class 4= Adult males

In many studies of alloparental care in anthropoid primates, pre-reproductive nulliparous females have been found to engage in more alloparental care than do members of other age/sex classes (see review by Nicholson, 1987). Such findings have engendered the most common explanation for the significance of alloparenting, that of "learning to mother", which was discussed in the introduction to this chapter. When examining the adjusted mean frequencies

("adjusted" refers to the number of individuals available in each age/sex class) of *all* alloparental behaviours for each age/sex class in the present study, young nulliparous females (juveniles and sub-adults) rank third after adult females without infants and other mothers (Table 1). Therefore, they do not perform more overall alloparental behaviours than do some other age/sex classes. However, when examining each type of alloparental care and socialization behaviour separately with respect to age/sex class, young females *do* rank higher than all other age/sex classes in terms of frequency of play with infants. The results of an analysis of each type of alloparental care and socialization behaviour is presented below.

Carrying of Infants by Alloparents

No significant difference was found with respect to frequency of carrying of infants with respect to age/sex class (Table III-2)

Table III-2: Frequency of Carrying of Infants

Age/sexclass	Observedmean frequency	Expectedmean frequency	O-E	$\frac{(O-E)^2}{E}$
Other mothers	1.4	0.7	0.7	0.7
Adult females without infants	0.5	0.2	0.3	0.4
Young females	0.5	0.4	0.1	0.0
Young males	0.1	0.4	-0.3	0.2
Adult males	0.0	0.7	-0.7	0.7

($\chi 2=2.0$, d.f.=4, $p>0.05$)

Other mothers tended to carry infants for a much longer period than did alloparents of other age/sex classes (Table III-3). Young females carried infants longer than adult females without infants or any male age/sex class. Adult females without infants carried infants for a very brief period on average.

Table III-3: Duration of Infant Carrying

Age/sex class	Mean duration of carrying bouts in seconds
Other mothers (n=15)	58.0
Adult females without infants (n=4)	6.3
Young females(n=8)	14.6
Young males(n=9)	0.2
Adult males(n=15)	0.0

Grooming of Infants

A significant difference existed in rates of grooming of infants according to age/sex class performing the grooming (Table III-4).

Table III-4: Rates of Grooming of Infants

Age/Sex class	observed mean frequency	expected mean frequency	O-E	$\frac{(O-E)^2}{E}$
Other mothers	20.2	20.0	0.2	0.0
Adult females without infants	23.7	5.3	18.5	64.5
Young females	13.2	10.6	2.7	0.7
Young males	7.1	11.9	-4.8	1.9
Adult males	3.8	20.0	-16.2	13.1

(χ^2 =80.2, df=4, p<0.001)

The greatest differences from the expected frequencies occur in the age/sex classes adult females without infants (18.5), and adult males (-16.2). Both other mothers and adult females without infants groomed infants most often, followed by young females, young males, and adult males.

Groom with infants

No significant difference was found with respect to mutual grooming with infants between classes of alloparents (Table III-5).

Table III-5: Rates of Grooming with Infants

Age/Sex class	Observed mean frequency	Expected mean frequency	O-E	$\frac{(O-E)^2}{E}$
Other mothers	1.1	2.0	-0.9	0.4
Adult females without infants	1.8	0.5	1.2	2.9
Young females	1.4	1.1	0.3	0.0
Young males	2.1	1.2	0.9	0.7
Adult males	0.6	2.0	1.3	0.9

($\chi^2 = 4.9$, df=4 , $p>0.05$)

Even though no significant difference was found between age/sex classes regarding grooming with infants, it is interesting to note that the mean frequency for young males (juveniles and sub-adults) are not only above the expected frequency for their age/sex class, but are also higher than all other age/sex classes. The rates for both sub-classes of adult females, which usually tend to be well above the expected frequencies in most alloparental and socialization behaviours, fall below the expected rates in this case.

Infants Exploring While Sitting on Alloparents

Infants performed this behaviour only while sitting on other mothers, therefore; no statistical tests were performed. Infants were observed to explore the environment while sitting on allomothers a total of 5 times during the study, much less frequently than on their own mothers (104 times).

Allonursing

Only one focal infant was observed suckling on another mother during the course of the study. The nursing allomother was a close companion of the infant's mother, and this particular animal had lost her own infant during its' second week of life. The abovementioned focal infant was noted suckling four times on the allomother, with the following durations: 46 seconds,18 seconds, 2 seconds, and 10 seconds. One non-focal infant in another group was seen involved in this behaviour fairly frequently after the allonursing mother lost her infant. Unfortunately, no focal animal data were collected on that particular infant, and frequencies and durations of its allonursing bouts are unknown.

Play with Infants

A significant difference was found with respect to mean *frequencies* of play with infants by the various age/sex classes (Table III-6).

Table III-6: Frequency of Play with Infants

Age/Sex class	Observed mean frequency	Expected mean frequency	O-E	$\frac{(O-E)^2}{E}$
Other mothers	0.5	3.4	-2.9	2.5
Adult females without infants	0.3	0.9	-0.6	0.4
Young females	6.1	1.8	4.3	10.3
Young males	4.4	2.0	2.4	2.9
Adult males	0.1	3.4	3.3	3.2

($\chi 2=19.3$,d.f.=4, $p<0.001$)

Mean rates of play with infants for both young females and young males are well above the expected frequencies for their respective age/sex classes. Frequencies for all of the adult age/sex classes fall considerably below the expected rates.

Young females and males contributed to nearly all of the observed *time* in which alloparents engaged in play bouts with infants (44.0% and 51.3% respectively) Data on infants playing with infants are not included here. Other mothers contributed to 4.0% of the total time, adult males 0.6%, and adult females without infants 0.1%.

Adult Male/Infant Interactions

Adult male *L.catta* do participate in some alloparental and socialization behaviours, although these occur at much lower mean frequencies than with other age/sex classes. Adult males also engage in occasional play bouts with infants, but were were never observed to carry infants, nor were infants ever observed to sit on adult males. Males were noted to groom infants a total of 57 times during the study, and to mutual groom with infants a total of 10 times. Infants were observed to locomote to and approach adult males three times, and to groom them three times during the course of observations. Play bouts between adult males and infants were noted twice during the study. Adult male/infant interaction began in week one, peaked during weeks 8 and 9, and continued through week 16; however, the frequency of such interactions were low during the last few weeks of the study.

Infant's Rank and Alloparental Care

No significant difference was found with respect to the frequency of alloparental behaviours received by infants of either low or high ranking mothers (Mann-Whitney U-test, U=7.0, p>0.05). However, individual differences were quite marked (Tables III- 7 and III-8).

Table III-7

Hourly Rate of Alloparental Behaviours Received by Infants

Low Ranking Infants	High Ranking Infants
CL=4.4 (Group2)	OR=3.3 (Group2)
ND=4.6 (Group1)	WN=4.6 (Group3)
WL=8.3 (Group3)	LL=4.7 (Group3)
	OL=5.2 (Group2)
	NC=7.2 (Group1)

Table III-8

Percentage of Infant's Total Observation Time in which it Received Alloparental Care

Low Ranking Infants	High Ranking Infants
CL=2.4%(Group2)	OR=1.9%(Group2)
ND=1.4%(Group1)	WN=2.9%(Group3)
WL=6.0%(Group3)	LL=2.8%(Group3)
	OL=3.1%(Group2)
	NC=4.1%(Group1)

WL, whose mother was the lowest ranking female in focal group #3, received the highest hourly frequency of alloparental behaviours in the two groups (a middle ranking infant received the highest hourly rate in the entire sample,WL ranked second in terms of hourly rate). Conversely, OR, the son of a high ranking female in group #2, received the lowest hourly rate of alloparental care for all focal infants. With respect to the amount of time in which infants received such care, WL ranked first, receiving the highest proportion of alloparental behaviours.The remaining two lower rankin, infants received relatively low proportions of care by conspecifics; however, their scores are similar to those of some high ranking infants.

Discussion

In her 1966 study of *Lemur catta* social organization, Jolly reports alloparental care in the form of grooming to newborns, performed almost exclusively by other mothers and occasionally by adult females without infants and juveniles, but not by adult males. In the present study however, behaviours designated as alloparental care and behaviours which assist infants in the socialization process were observed to occur in all age/sex classes. Some infant care behaviours, such as allonursing, or allowing infants to explore and play while sitting on the alloparent, involved one particular age/sex class exclusively (other mothers); some were performed notably more often by individuals of one age/sex class than another; and others were performed by all members of all age/sex classes in the troop.

Hinde (1974) and Nicholson (1987) point out that because alloparental care varies interspecifically to such a great extent, costs and benefits to the mother, infant, and alloparent should also be viewed as highly variable. When

examining all alloparental and socialization behaviours together, other mothers, as well as adult females who did not reproduce that particular year, engaged in such behaviours most *frequently* , and a significant difference between all adult females and all other age/sex classes was found to exist. Other mothers, but not adult females without infants, contributed the most *time* to alloparental care. When looking at each type of behaviour separately, all adult females groomed infants significantly more frequently than animals of other age/sex classes. Two alloparental behaviours, allonursing, and allowing infants to explore or play while sitting on the alloparent, were performed exclusively by other mothers. Allonursing was observed to occur infrequently, and involved only one focal infant who occasionally suckled on a companion of her mother's who had lost her own infant. Allonursing was also seen between a non-focal infant and an adult female who had also lost her offspring.

McKenna (1979) suggests that the activity of infant transfer among Colobines exposes the neonate to a wide variety of female social contacts other than the mother, and that this aids in the development of adult social relationships independent from those of the mother. Although infant transfer was not observed among *Lemur catta* females, much contact between young infants and adult females does occur, and McKenna's notion that contact may assist infants in the development of social relations with females in the natal troop may be suggested as one explanation for the high degree of infant/adult female interaction in ringtail lemurs.

The amount of alloparental care exhibited by particular age/sex classes in the present study are similar to those of Zucker and Kaplan (1981), who found that among patas monkeys, adult females engaged in the highest proportion of alloparental care, followed by immature animals. The authors suggest that the

adaptive value for the high incidence of alloparental care in this species is that in potentially dangerous situations patas monkeys responded by high speed locomotion, and an infant in proximity to any adult female will benefit by being carried by her. Although *Lemur catta* are not as terrestrial as patas, they are one of the most, if not *the* most terrestrial of the prosimians, spending at least 30% of their day on the ground (Sussman, 1977). *Lemur catta* respond to danger or inter-troop encounters by rapid locomotion and chasing. Although rates of infant- carrying by alloparents were low, infants were, at times, carried by other mothers, adult females, and young females during at least part of a troop progression. Other mothers were found to have both the highest frequency and duration of infant carrying. In potentially dangerous situations, such as aerial predators (raptors) circling overhead, infants were occasionally observed jumping onto a female other than the mother when the troop alarm call was given, if the mother was not in the immediate vicinity of her infant.

Thus, it appears as though a *Lemur catta* infant can benefit from a high degree of female/infant interaction with respect to both developing relationships with females in the natal troop, and protection and assistance in dangerous situations. For the adult female, alloparental care given to infants can be seen as aiding kin, since the core of the social group is made up of females and their female descendents (Richard, 1987). Unfortunately, since genealogical relationships were not known for animals in the focal troops, it is not possible to explain specific allomother/infant dyads as existing due to degrees of relatedness.

The primary benefit to the mother of alloparenting appears to be that of mother relief (Gray, 1985), as infants were observed exploring and playing while sitting on other mothers, being carried by other mothers, adult females, and young

females and males, and being groomed by animals of all age/sex classes while off the mother. Such activities gives *Lemur catta* mothers free time to forage, self groom and rest.

The most common explanation for the significance of alloparenting by juvenile and sub-adult female primates is that of gaining maternal experience before reproduction (Lancaster, 1971; Hinde, 1974; Hrdy, 1976; Nishida,1983; Gray, 1985). Nicholson (1987) argues that allomothering appears to have a specific developmental function in young female primates. Hrdy (1976) suggests that allomothering by pre-reproducive females helps to decrease the disparity in maternal competence between primiprous and multiparous mothers.

In *Lemur catta* , juvenile and sub-adult females (termed "young females") were observed to perform a number of behaviours which can be considered alloparental, as well as behaviours which can be seen as assisting in the socialization process of infants, including carrying and grooming infants, mutual grooming with infants, and engaging in social play with infants. Young females demonstrated the highest rates of social play with infants for all non-infant age/sex classes, and showed the second highest rates of infant carrying and grooming with infants.

Although mutual grooming with infants may not be considered an alloparental behaviour, it nevertheless appears to be a significant aspect of infant socialization. Grooming in *Lemur catta* is an important social activity. During rest periods animals of all age/sex classes engage in long social grooming bouts. By spending time grooming with conspecifics, the infant is able to become familiar with kin, peers, and other conspecifics, and thus becomes integrated into the social group as as independent animal and not simply part of a mother/infant dyad.

Social play between alloparents and infants should also be regarded as an interaction which assists infants in the socialization process, because through such activity, infants are able to become acquainted and form relationships with conspecifics, learn appropriate responses to group members, and acquire useful social skills. There appeared to be a definite qualitative difference, on the part of young females, between social play with infants and social play with age mates, the former being much slower and gentler. For young females, social play with infants provides them with the opportunity to become accustomed to handling and carrying infants.

Although play and grooming with infants, both "socialization" rather than strictly "alloparental" activities, were performed most frequently by young females, such females were also observed to engage in infant care activites such as carrying and grooming infants. In fact, young females rank second with respect to both rate and duration of infant carrying (Table 3) as well as second in overall proportion of alloparental care in terms of age/sex class (Figure III-1). Thus, I suggest that considering the large amount of time and relatively high frequency of alloparental and socialization behaviours observed in juvenile and sub-adult female *Lemur catta* , this species should be included among those to which the "learning to mother' explanation can be applied.

Juvenile and sub-adult males were observed to groom to and with infants, and to engage in social play with infants. Young males demonstrated the highest overall rate of grooming with infants and ranked second after young females with respect to rates of social play with young

L. catta . Since *L. catta* males have been noted to engage in troop transfer when they reach sexual maturity because they have limited access to breeding females in their natal troop (Jones, 1983), it would be unlikely that such males

would interact with infants in order to establish a bond with the mother for purposes of enhanced reproductive success. Thus, interaction between pre-reproductive males and infants might be explained in terms of kinship. Nicholson (1987) suggests that the greater involvement of siblings and closely related females in infant care may be a reflection of both the mother's and infant's greater tolerance of care by animals least likely to abuse the infant. This notion could also be applied to male siblings and thus could serve as an explanation for the existence of alloparenting and interactive behaviours observed in young males.

Adult Male Alloparental Care and Male-Infant Interaction in *L. catta*

As mentioned earlier, Jolly (1966) does not report interaction between adult males and infants. However, during a later study at Berenty, Jolly (1971, unpublished manuscript) observed an adult male adopt a 30 to 40 day old abandoned infant for a period of two days before it disappeared, presumably having died of starvation. Caretaking behaviours performed by the adult male included dorsal and ventral carrying, clasping the infant, grooming, allowing the infant to suck on tufts of the males' fur, and retrieving the infant when it was scraped off of his dorsum by a branch. Sussman (1977) observed that adult male *L. catta* tolerate infants playing around them, but otherwise reports little interaction between adult males and infants.

Although the amount of alloparental care and positive interaction with the infant is much less than that of other alloparental age/sex classes (as outlined in the Results section), the data suggest that adult *L. catta* males *do* play a small part in the care and socialization of the infant.

Whitten (1987) outlines five categories of adult male/infant interactions in primates: intersive caretaking; affiliation; occasional affiliation; tolerance; and use and abuse. In those interactions determined to be affiliative, Whitten states that the average overall rate of interaction is low, but that within specific male/infant pairs the frequency of affiliation is much higher. The author notes that in species showing affiliative relationships, males have been observed to hold, cuddle, groom, nuzzle, and examine infants. In species where males display occasional affiliation, Whitten states that males are generally indifferent, yet under particular circumstances they engage in affiliative behaviours with specific infants.

I suggest that the adult male/infant interaction observed in *L. catta* in the present study could be classified as "occasionally affiliative". Interactions such as grooming to and with infants and engaging in social play were not observed to occur on a regular, predictable basis, nevertheless they were observed occasionally, as noted above.

The significance of the occurrence of male/infant interaction in *L. catta* could be explained by two possible factors. First, such affiliation could be seen as a mild form of parental investment, although paternity testing would be needed in order to corroborate this suggestion. Since not all adult males engage in annual troop transfer (Jones, 1983), males could be interacting with their own offspring. I observed (on an unrecorded, anecdotal basis) adult males occasionally wave their tails and squeal at an infant (a threat gesture) who was sitting dorsally on the mother when the mother could not see the male. In all observed cases of such behaviour, the mother turned and cuffed the offending male as soon as the threat gestures began. This behaviour has also been observed in semi-free ranging *L. catta* at the Duke University Primate Center (Pereira, personal

communication). It seems unlikely that the father of an infant would direct such behaviour towards his own offspring. In light of these types of threat displays, it seems unlikely that an adult female would allow a male who was unrelated to her infant to contact, touch, or groom it.

Second, since not all males switch troops annually, male/infant interaction may be a strategy on the part of the male to develop a bond with the mother in order to increase opportunities for future reproductive success. Whitten (1987) suggests that male affiliation with infants may enhance a male's mating success and notes that a number of studies have demonstrated that throughout the primate order, male/infant affiliations are often accompanied by bonds between the mother and the male. She states that an affiliation with an infant may help the male to establish a relationship with the mother, or it may be an extension of an established male/female relationship. One point that should be considered, however, is Smith and Peffer-Smith's (1984) argument that male-immature interactions may be a byproduct of the high degree of sociality found in primates, and might not, by themselves, have a particular adaptive significance.

Alloparental Care and Infant's Rank

In some species, such as baboons and vervet monkeys, infants of high ranking mothers have been noted to receive more alloparental care (Cheney, 1978; Whitten,1982, cited in Nicholson, 1987), while in other species, such as bonnet macaques, infants of low ranking mothers have been observed to receive more attention from alloparents,but the alloparents were often abusive (Silk, 1980). Conversely, a number of researchers have found that maternal rank was not a factor in the frequency of alloparental care (Hrdy, 1977; Nishida, 1983). The findings from the present study correspond to the latter pattern as

amount of alloparental care was not found to correlate with infant's rank. The lowest ranking infant in one of the focal groups received both a higher rate and proportion of alloparental care than did any of the high ranking infants, and the remainder of the low ranking infants received rates and proportions of alloparental care which were comparable to some of the highest ranking infants. Since genealogical relationships are not known for *L. catta* at Berenty, one can only speculate that perhaps the high degree of variability in alloparental care among infants is related to the number of siblings and other close relatives that an infant might have at any given time, as well as the number of companions a mother might have, regardless of her rank. It does appear clear however, that the rank of an infant has no bearing upon the extent to which it will receive care by conspecifics.

Conclusions

A number of conclusions can be made with respect to the present study of alloparental care and affiliative interaction with infants by conspecifics other than the mother in free-ranging *Lemur catta*.

1. All age/sex classes were found to participate to varying degrees in alloparental care and/or socialization of the infant.

2. Other mothers and adult females without infants demonstrated the highest overall *rates* of alloparental care. Other mothers contributed the most *time* to alloparental behaviours in relation to all other age/sex classes.

3. Significant differences between age/sex classes were found with respect to frequencies of grooming of infants and social play with infants. All adult females groomed infants significantly more frequently than did animals in other age/sex classes. Juvenile and sub adult females and males engaged in

social play with infants significantly more frequently than did other group members.

4. Significant differences were *not* found with respect to the frequency of mutual grooming with infants, and carrying of infants, although other mothers carried infants more often than other group members and juvenile and sub-adult males engaged in mutual grooming with infants more frequently than did animals of other age/sex classes.

5. Adult males did not carry infants, but did engage in grooming of and with infants, and occasional social play with infants. Although the frequency of such behaviours were low compared to to other age/sex classes, I suggest that adult males *do* play a small role in the care and socialization of infants.

6. Infant's rank was not found to have an effect upon the amount of alloparental care it received.

7. Proposed benefits to infant *L. catta* of alloparental care include:

a. The opportunity to develop relationships and acquire social skills with conspecifics other than the mother. Since *L. catta* infants are developmentallyprecocial, and are nearly independent of their mothers at 16 weeks of age, the infant must begin to develop relationships with others and learn its' place in the social group from a relatively much earlier age than do infants of anthropoid species.

b. Protection in the form of rescue in dangerous situations should the mother not be in the immediate vicinity of her infant.

8. The primary benefit to the mother of allowing conspecifics to engage in alloparental and socialization behaviours with her infant appears to be that of "mother relief", (ie: providing the mother with free time to forage and rest while her infant is interacting with others).

9. Proposed explanations for the adaptive significance of alloparental and socialization behaviours in *Lemur catta* include:

a. Aid to kin, since all females and pre-reproductive animals within a social group are related.

b. Learning parental skills with respect to infant care and interactive behaviours performed by juvenile and sub-adult females.

c. A mild form of parental investment on the part of the adult male in relation to male/infant interactions; however paternity testing would be needed to confirm such a suggestion.

d. A strategy on the part of the adult male to establish a relationship with the mother, which may enhance future reproductive success.

To conclude, although *Lemur catta* appear to be the only prosimian species for which alloparental care has been closely examined, they may not be alone with respect to this phenomenon in the sub-order *Prosimii*. Future quantitative studies concerning interaction between infants and conspecifics in other prosimian species living in various types of social organization are necessary in order to gain a broader understanding of types of infant/conspecific relations as well as adaptive reasons for such interactions within the sub-order *Prosimii*.

Since social organization and environmental niche appear to be important factors in determining whether or not and to what extent alloparental care exists in a species, future studies of alloparental behaviour in prosimians must consider the type of social organization found in the study species, which group members (age-sex classes) interact with and care for infants, and what selective pressures may be operating to result in a particular pattern of alloparental care. For example, a future study might consider whether or not alloparental care in a

primarily arboreal multi-male/multi-female species, where the infant would presumably not venture off the mother until its' physical coordination and locomotor abilities were reasonably well developed, would begin later and consist of different types or rates of such care than in a more terrestrially adapted multi-male/multi-female species. Another research possibility would be to compare patterns of infant care in a nocturnal and diurnal mongamous species, such as *Avahi* and *Indri*. Among anthropoid species displaying monogamous social organization, the father is the primary caregiver (for example, marmosets (Box,1975,1977), owl monkeys (Dixson and Fleming,1981; Wright, 1984), titi monkeys (Wright, 1984),siamangs (Chivers, 1974). Thus, a study of parental care in species such as *Indri*, *Avahi*, and *Lemur mongoz* would contribute to the existing knowledge of caregiving patterns in monogamous primate species. With more and more field research being undertaken at present on previously unstudied prosimian species, particularly Malagasy primates, we may, in the near future, gain new knowledge concerning the phenomenon of alloparental behaviours in prosimians.

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Chapter 4: Conclusion

Problems in the Study of Primate Infant Social Development and Alloparental Care: Suggestions for Future Studies

Infant Social Development

Much interest has been shown among scientists in the study of social developmental processes in the primates (see Baldwin, 1969; Box, 1975; Hoff, Nadler & Maple, 1981; Berman, 1982; Nicholson, 1982; Lee, 1984; Rhine, North, & Westlund, 1984). Nicholson (1982) argues that a successful primate adult in any species must know the rules of the species, know what to expect from its conspecifics, and have the social skills to form alliances within the social group. By observing how a young primate develops socially, we can, perhaps, gain insight into the social organization of a particular species. Indeed Poirier (1972) suggests that it is useful to attempt to discern how a young primate's learned social relationships with conspecifics affect its behaviour, and eventually through such behaviour, the social order. Through such research, a picture of both interspecific similarities as well as differences within the order can be seen, and comparisons of social development between the primate and other mammalian orders can be made. From an anthropological standpoint we can see how varying adaptations to differing environments and types of social organization can affect the social development process in both human and non-human primate groups.

Problems in the Study of Infant Social Development

It is far easier to study and monitor the social development of infant primates in captivity, and much important work has been done in captive situations,

particularly with species which would be difficult to follow in the wild, for example marmosets (Box, 1975), owl monkeys (Dixson and Fleming, 1981), and cotton-top tamarins (Cleveland and Snowdon, 1984); or species with a very lengthy social developmental period, such as lowland gorillas (Hoff et al., 1981). Nonetheless, it is also important to look at species in non-provisioned, wild situations, in order to gain an idea of natural infant mortality, and to determine whether the development of social relations and social independence differ from animals in captivity when the infant must face environmental realities. Because in some species, particularly the larger bodied old world monkeys and apes, development from total dependency on the mother to complete independence can take a number of years, it is difficult to set up studies which would monitor the developmental process over such a long period of time.

Visibility in field situations presents yet another problem with respect to the logistics of studying the social development of primate infants, as many species are highly arboreal, and some both arboreal and nocturnal, making it a difficult or impossible task to identify infants. Furthermore, it is usually not feasible to attempt to mark small, young infants. The latter reasons could serve as an explanation as to why so little is known about the social development of prosimian primates, which make up eight of the fifteen primate families and constitute 34 individual primate species (excluding *Tarsiiformes*). Many prosimians are very small bodied even as adults, relative to most anthropoid species, and most are nocturnal; thus it would be a very difficult task to follow a tiny infant in the dark, high in the canopy, and try to gain a sense of its developmental progress.

Chapter two of this thesis focused on the social development process in one of the larger bodied, diurnal, and highly terrestrial prosimian species, *Lemur catta*. Because of the three variables mentioned above, it was fairly easy to identify, sex, determine the rank of, and follow a sample of eleven infants in a wildlife reserve where little to no hunting and minimal predator pressure occurred.

Infant Social Development in *Lemur catta*

My study revealed that infant *Lemur catta* are nearly independent of their mothers by 16 weeks of age. They are able, at this point in their development, to forage and locomote independently, relate with others as an independent member of the social group rather than as part of a mother-infant dyad, and display some adult sex-specific behaviours, particularly during social play. Furthermore at this age they are subject to dominance relations by conspecifics. Neither sex nor rank differences were found in terms of measures of independence, characterized by behaviours such as environmental exploration, independent arboreal and terrestrial progression, independent foraging and drinking at the water source, grooming of and with conspecifics, and social play. Rank differences were found, however, with respect to measures of dependence on the mother, with lower ranking infants tending to ride and sit on the mother more frequently, suckle more often, and engage in behaviours such as foraging and exploration of the environment while sitting on the mother more frequently than higher ranking infants. Lower ranking infants also emitted lost calls and searched for the mother at a higher frequency than did infants of higher ranking mothers.

Sussman (1977) who described some general developmental stages in free-ranging *Lemur catta* and *Lemur fulvus rufus*, states that infant *L. catta* are more precocial than *rufus* infants, and found notable differences between the two species with respect to developmental markers such as ventral to dorsal riding, independent environmental exploration, increasing time off the mother, and independent locomotion, in terms of the age (week of life) at which infants commence these behaviours. He suggests that the high degree of arboreality found in

L. f. rufus, and thus, the danger of falling, is one possible reason that *L.f.rufus* infants develop more slowly. Conversely, he postulates that there may be selective pressures on terrestrially adapted species for earlier locomotor independence, particularly in species with long day ranges such as *L. catta*.

One might predict that with such marked differences occurring in infant social development between two species of the same genus, equal or even greater differences might occur between other diurnal prosimian species. The developmental stages proposed by Fragaszy and Mitchell (1974) and Poirier (1972,1974), and used as a framework in which to examine infant social development in *Lemur catta* in the present study, could be used as a guideline in which to make intra-specific comparisons of infant social and behavioural development among prosimians in future studies. Although the abovementioned guidelines are fairly general, they cover important developmental markers and were found useful in the present study in terms of looking at the precociality of *L. catta* in relation to anthropoid species in which the social development of infants has been examined. However, not all prosimian, and in particular not all Lemuriform species are necessarily more precocial than many species of anthropoid (for example, smaller bodied New

and Old world monkeys), and further studies are needed to determine rates of social development in order to make developmental comparisons with both prosimian and anthropoid species. For example, weaning conflict was examined in the present study, and it was found that rejections from the nipple began in the 8th week of life and rejection from dorsal riding in the 12th. However, *Lemur catta* are a largely terrestrially adapted species, unlike most other lemurs, and selection for rapid locomotor development in infants may be operating as is suggested by Sussman (1977, noted above). Thus, weaning (especially from dorsal riding) in this species very likely occurs earlier than among chiefly arboreal lemur species.

Furthermore, factors such as body size and social organization may affect the social development of infants. In multi-male/ multi female species where much infant-conspecific interaction and alloparenting occurs, the social development of infants, and the acceptance of infants as independent members of the social group might be not only more rapid, but qualitatively different (in terms of opportunities for infants to develop relationships with many group members) than in a species with a different social organization. Differential rates of development among prosimian species should be examined in the context of what environmental and social variables have contributed to the selection for a particular pattern and rate of social development found in the study species.

Thus, it appears that in future, studies of infant social development must be carried out on prosimian species, particularly in natural field situations where logistically possible, in order to properly compare the social development of prosimian infants with each other and with anthropoid species, as well as to remedy the paucity of information concerning infant social development in the prosimian sub-order.

Alloparenting and Infant-Conspecific Interactions

A fair number of studies have concentrated on patterns and types of alloparental care in anthropoid species with a relatively good representation from free-ranging groups. For example, black howler monkeys (Bolin, 1981), patas monkeys, (Zucker and Kaplan, 1981) rhesus macaques (Berman, 1982), and chimpanzees (Nishida, 1983).

Jolly (1966) reported that alloparental care in *Lemur catta* involved almost exclusively other mothers, and occasionally nulliparous adult females and juveniles. However, my study revealed that various forms of alloparental care and infant-conspecific interactions exist among all age/sex classes (see Chapter 3 Discussion). Other mothers and adult females without infants participated the most frequently in alloparental care; however, both juvenile and sub-adult females and males, and even adult males, engaged to varying extents in care and interaction with infants. I concluded that kin selection , opportunity to learn parental skills (in the case of alloparenting by young, pre-reproductive females), and a possible strategy to enhance reproductive success (in the case of male-infant interaction) can be used to explain why group members of various age/sex classes engage in alloparenting and interaction with infants. *Lemur catta* mothers benefit from such activity by gaining free time to rest and forage while their infants are in the care of others. The

advantages to infants of alloparental care can be seen as protection by conspecifics if a dangerous situation should arise and the mother is not immediately available, as well as the opportunity to develop social skills and relationships with other group members.

Perhaps Jolly's (1966) findings differ from the present study because while my study focused exclusively on infants, their social development, and who

interacted with them, Jolly's pioneering study of *Lemur catta* dealt with more general aspects of social organization and behaviour in the species.

Problems and Important Considerations in Alloparenting Studies

Intra-troop competition between mothers, social organization, and environmental niche appear to be important determining factors in terms of whether or not and to what extent alloparenting exists in a primate species (see McKenna, 1979; Nicholson, 1987; Whitten, 1987; as well as chapter 3 of this thesis). If, for example, food resource competition between mothers is great, such females may be reluctant to allow other mothers to handle their infants. Which group members are available for infant caregiving is also important. Furthermore, factors such as the relative arboreality or terrestriality of a species might affect how much alloparental care infants receive. These aspects should be considered in future studies.

In studies of species in the wild displaying alloparental care, intra-troop relatedness is generally not known, unless the particular group has been the focus of a longitudinal study. Thus, in most cases, it is impossible to determine, for instance, if an infant is receiving alloparental care from a close relative, such as a grandmother, full sibling, or father, or from an unrelated animal such as a female companion of the mother or perhaps a male who is attempting to create a bond with a particular infant's mother. This constraint confounds attempts to determine with any sense of confidence the adaptive significance for the existence of alloparental behaviour in primate groups whose members have not been the focus of extensive, long-term studies.

Adult Males and Infants

Male-infant interactions and patterns of male care have been the focus of numerous recent studies (see review by Whitten, 1987). In the present study it was found that males interact more with infants than was previously reported by Jolly (1966) . An important consideration in terms of future studies of male-infant interaction is Whitten's (1987) statement that in many cases, males have been reported simply to "tolerate" infants, but otherwise show no interest in them; but that such a classification

> "may reflect the current lack of knowledge more than the absence of male attention to infants" (page 350-351).

One possibility for a future study of male-infant interaction in prosimians would be to look at males and infants in the remainder of the genus *Lemur*, since Jolly (1971 unpublished manuscript) reports that adult male *L. fulvus* have been noted to sleep with and groom infants in a captive situation when the mother has been artificially removed. It would indeed be interesting and of value to investigate whether or not *L. fulvus* males display similar behaviour in a natural situation with the mother present. Another possibility would be to examine monogamous prosimians such as *Indri*, and *L. mongoz*, since extensive male care exists in a number of monogamous anthropoids. There is also no information as yet on male-infant interaction in diurnal prosimian species which live in small social groups in which the exact social organization has yet to be determined, such as *Varecia* and *Hapalemur*. Male parental care has been observed in semi-free ranging *Varecia variegata* at the Duke University Primate

Center (Kaufman, Pereira, Wright, personal communication; personal observation), and if it were logistically possible to conduct a study of alloparenting in wild *Varecia* , the results might prove useful in terms of gaining a clearer picture of alloparental care throughout the prosimian sub-order.

Thus, it appears that much room still remains for investigations of both infant social development and alloparental care in prosimians. Considering the extensive variation in group composition, social organization, and environmental niche found among this sub-order, and the extent to which such variation may affect social development and patterns of alloparenting, future studies in the above areas have the potential to contribute greatly to the existing primatological literature.

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Appendix 1

August and December 1987 census of three *L.catta* troops in Reserve #3 at Berenty Natural Reserve, Madagascar

	Group 1	Group 2	Group 3
adult females			
Aug.	7	5	8
Dec.	7	5	8
adult males			
Aug.	6	8	5
Dec.	4	7	4
sub-adult females			
Aug.	2	3-4 juv.& sub-ad. animals	3-5 juv.&s.a.
Dec.	2	1	1
sub-adult males			
Aug.	1	see above	see above
Dec.	2	2	2
juvenile females			
Aug.	2	see above	see above
Dec.	2	1	1
juvenile males			
Aug.	1	see above	see above
Dec.	1	1	1
infant females			
Aug.	0	0	0
Dec.	3	1	2
infant males			
Aug.	0	0	0
Dec.	3	3	3
infant sex unknown			
Aug.	0	0	0
Dec.	1	0	1

The above figures reflect troop population changes after birth season (late August to November) and adult male transfer (Sept. and October).

Appendix 2 Ethogram

Operational Categories*

On the mother behaviours
- ventral carry
- dorsal carry
- ventral sit
- dorsal sit
- suckle
- test forage on mother
- forage on mother
- observe environment on mother
- explore mother
- explore environment on mother

With the mother behaviours
- ventral carry
- dorsal carry
- ventral sit
- dorsal sit
- suckle
- test forage on mother
- forage on mother
- observe environment on mother
- explore mother
- explore environment on mother
- locomote to mother
- play bite to animal (mother)
- locomote to another animal (mother)
- locomote off mother
- groom by (mother)
- social (rough and tumble) play (with mother)

Dominance and agonistic behaviours
- cuffed by animal (age/sex class)
- submissive chatter
- fight with (age sex class)
- mother can't get to infant
- displaced by
- displace to

Weaning conflict behaviours
- nipple reject
- dorsal carry reject
- reject from other (e.g. grooming by inf.)

Independent behaviours
- locomote off mother
- locomote progression arboreal
- locomote progression terrestrial
- forage off mother
- explore environment off mother
- groom to another animal (age/sex class)
- social (rough and tumble) play (age/sex class)
- solitary play
- drink
- mutual groom with animal (age/sex class)
- stink fight practise
- branch marking practise

Dependence behaviours
- ventral carry
- dorsal carry
- ventral sit
- dorsal sit
- follow mother
- seek nipple
- suckle
- lost call
- search for mother
- test forage on mother
- forage on mother
- observe environment on mother
- explore environment on mother
- retrieved by mother

Solitary self-maintainance behaviours
- forage off mother
- drink off mother
- self-groom

Alloparental and affiliative behaviors
- ventral carry by another animal (age/sex class)
- dorsal carry or sit on another animal (age/sex class)
- groom by (age/sex class)
- groom to another animal (age/sex class)
- mutual groom with another animal (age/sex class)
- suckle on another mother
- explore on another mother
- social (rough and tumble) play (age/sex class)

*behavioural units may appear in more than one category